


# **The Impact of Injuries on Free-living Chimpanzees**

**How injury effects the social behaviour, mother-  
dependant behaviour and the locomotion of adult female  
chimpanzees from the Sonso community, Budongo Forest  
Reserve, Uganda.**

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**This thesis is submitted for the degree of Master of Philosophy,  
School of Archaeology and Anthropology  
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Except where otherwise indicated,  
the work presented in this thesis is entirely my own.

A handwritten signature in dark ink, appearing to read 'Julie Munn', with a stylized, flowing script.

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## **Abstract**

Many chimpanzees in Uganda are accidentally killed or maimed when caught in hunter's snares that are set throughout forest areas. Chimpanzees are not the target species hunted, but are frequently caught. In field sites across Uganda, where chimpanzees are studied, at least 22% of identified community members have known or suspected snare related injuries. In the Sonso community, Budongo Forest, nine of the 49 community members have serious injuries from snares. The injuries range from missing limbs to twisted and mangled digits.

This study focuses on 12 of the adult females from the Sonso community, five of which have deformities to limbs. This thesis examines the effect these deformities have on four primary behavioural parameters – group structure and association patterns, mother-infant relationships, grooming behaviour, and locomotion. 451 focal animal samples were collected over an eight-month study period on both injured and non-injured adult females.

Although the wounded chimpanzees in this study have survived their injuries, this study shows that there are behavioural effects resulting from those injuries. Injured female chimpanzees, when compared to non-injured females, were found more frequently in small groups, including time alone with their dependants. They also spent more time in arboreal space. Injured mothers gave less support, than non-injured mothers, to their dependants once they had reached an age where they were able to feed and travel independently. Injured and non-injured mothers cared for very young chimpanzees equally. Chimpanzees with more extreme injuries spent less time travelling than less injured or non-injured chimpanzees, which suggests that severely injured chimpanzees are more greatly affected by their injuries. Chimpanzees with injuries spent less time grooming others, but were groomed by others equally when compared to non-injured chimpanzees. Injured individuals were well tolerated in the community, with injured females being equally likely to associate with other injured or non-injured females.

These changes in behaviour are argued to be a result of the physical difficulties associated with an injury, rather than because of any lack of tolerance shown by other community members. Injured females spent more time alone, which may have long-term social consequences, such as a lower reproductive rate, or a greater risk of mortality, which may affect the overall population growth. This in turn has implications for the conservation of an endangered species.

As long as snaring continues in Ugandan forests, the risk of injury, or death from snare wounds continues. If chimpanzees are snared a second, or even third time, the effects these injuries have on the behaviours described above will increase. Hunting in forest reserves is illegal in Uganda, but further measures must be taken in order to reduce the incidence of snaring. These measures could include continuation of snare removal and education programs, providing alternate income for hunters, and promoting the farming of domestic meat to supply additional protein sources to replace bush meat.

For Sophie,  
who introduced me to the world of chimpanzees.

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# Chapter One

## Introduction

The aim of this thesis is to assess the effects injuries have on the social, mother-infant and locomotor behaviour of wild chimpanzees living in the Budongo Forest Reserve, Uganda. The prediction is that some behaviours will be altered because of the physical impairments of the chimpanzees. It is hoped that studies of this nature will create a better understanding of how injury may affect behaviour, and that this information will be useful for conservation and education programs aiming to conserve and protect the welfare of wild chimpanzees in Uganda.

The aim of this chapter is to give a brief overview of chimpanzees in the wild, the threats to their survival, the issue of hunting and the consequent 'accidental' snaring in Uganda. Research aims and an overview of the structure of this thesis appear at the end of this chapter.

### 1.1 Taxonomy, distribution and habitat of *Pan troglodytes*

Chimpanzees are customarily divided into two species: the bonobo or pygmy chimpanzee (*Pan paniscus*) and "the chimpanzee" or common chimpanzee (*Pan troglodytes*). *Pan troglodytes* has historically been divided into three subspecies: *P. t. schweinfurthii*, *P. t. troglodytes* and *P. t. verus* (Groves 2001). A fourth subspecies *P. t. vellerosus* has recently been recognised using mitochondrial DNA analysis (Gonder et al. 1997).

The current distribution of *Pan troglodytes* is thought to extend through approximately 21 countries in equatorial Africa (Edroma et al. 1997). *P. t. troglodytes* covers the central part of this range, from the Congo River mouth north into Cameroon, into Nigeria east of the River Niger (unless *P. t. vellerosus* is found here: see below), and into the Central African Republic east to the River Oubangui (Groves 2001). *P. t. verus* is found in the western part of the range, from Senegal to the Volta or the Dahomey Gap (Groves 2001). *P. t. schweinfurthii*

is the eastern subspecies that exists in Democratic Republic of Congo (DRC), north of the River Congo and east of the River Lualaba, into Sudan, Uganda, Rwanda, Burundi, and Tanzania (Groves 2001). The most recently recognised sub-species *P. t. vellerosus* comes mainly from Nigeria, having populations on both sides of the Niger River (Boesch & Boesch-Achermann 2000), so it combines what would have previously been regarded as the westernmost *P. t. troglodytes* and the easternmost *P. t. verus*. Chimpanzees live in both forest and woodland habitats throughout their range.

## **1.2 Field work on chimpanzees**

Field studies of *Pan troglodytes* began seriously in the early 1960s with Jane Goodall's study in the Gombe Stream National Park, Tanzania; Vernon and Frankie Reynolds' study in the Budongo Forest, Uganda; and a study by Kortlandt in what was then the Belgian Congo (Goodall 1968, 1986; Kortlandt 1962; Reynolds 1963; Reynolds 1965; Reynolds & Reynolds 1965). The research at Gombe has been continuous since 1960, whereas the chimpanzees at Budongo Forest have been studied infrequently (Sugiyama 1968; Sugiyama 1969) until 1990, when Reynolds returned and initiated the Budongo Forest Project (Reynolds 1990), where research is now ongoing. Currently there are many other long-term field studies of chimpanzees including research at the Mahale Mountains National Park, Tanzania, which commenced in 1965 and has continued since that time (Nishida 1968, 1979, 1990), and research on chimpanzees at Kibale National Park, Uganda, which began with a study by Ghiglieri between 1976 and 1981 (Ghiglieri 1984), and later followed by Wrangham in 1987 (Wrangham et al. 1992). In West Africa two sites well known for chimpanzee field studies are: the Taï chimpanzee project in the Taï National Park, Côte d'Ivoire, which began in 1976 with its first long-term study beginning in 1979 (Boesch & Boesch-Achermann 2000), and Bossou, Guinea, where a chimpanzee project was initiated in 1976 (Sugiyama 1979, 1981).

### 1.3 Behaviour of chimpanzees

Chimpanzees have been described as rumbustious, extroverted and excitable with respect to their social behaviour (Napier & Napier 1985). They have a fission-fusion social system that allows for individuals to group together, or disperse at will, so group sizes are constantly changing (Goodall 1986; Nishida 1968; Sugiyama 1968). The size of a community remains stable, with the exception of deaths, births and migrations, and generally is from 20-30, to over one hundred individuals (Boesch & Boesch-Achermann 2000; Nishida 1990). Generally males remain in their natal groups and it is the females that immigrate to neighbouring communities, with communities being defended by groups of adult males (Goodall 1986).

Chimpanzees are terrestrial and arboreal, feeding and resting both on the ground and in the trees, although they generally travel long distances on the ground. A night nest is built every night unless a previous nest is re-used, and day nests are quite commonly built for resting and sleeping (Brownlow et al. 2001).

Chimpanzees have a predominantly frugivorous diet (Isabirye-Basuta 1989), but also eat leaves and flowers (Newton-Fisher 1999a), insects (Goodall 1986; Newton-Fisher 1999b) and nuts (Boesch & Boesch-Achermann 2000). They hunt and eat meat, including red colobus monkey (*Colobus badius*) (Mitani & Watts 2001; Stanford et al. 1994), black and white colobus monkey (*Colobus guereza*) (Newton-Fisher 1999a, personal observation), and *Cercopithecus* monkeys (Kanyuyni Basabose 2002; Newton-Fisher 1999a).

Grooming plays a part in many aspects of the social behaviour of chimpanzees (Simpson 1973). It also serves the function of cleaning the hair and skin and removing ticks or other ectoparasites. Self-grooming is also common, and increases in frequency with age (Goodall 1968). Communication is an important part of the social life of chimpanzees with vocalisations used frequently between dispersed groups of the community. A wide range of visual signals are also used including facial expressions, intimidating displays and postures (Goodall 1968).



Chimpanzees from many field sites across Africa show behavioural patterns with significant cultural variation. Behaviours such as termite fishing, ant fishing, use of a probe to extract liquid, nut cracking, rain dancing, and the use of leaves for various purposes such as grooming are all described as being customary or habitual in some chimpanzee communities, but absent in others (Whiten et al. 1999).

Reproduction is similar to that of humans (Napier & Napier 1985). Menstrual cycles last on average 39.8 days for young nulliparous females and 33.8 days for older multiparous females (Wallis 1997). Females exhibit their first sexual swelling at around 10 – 11 years, with an average duration of maximal swelling of 12 – 13 days (Wallis 1997). Duration of gestation ranges from 208 days to 235 days, with an average of 225.3 days (Wallis 1997). Mating is generally promiscuous, although consortships involving just one male and female have been recorded (Goodall 1986). Males begin copulating from a young age (Nishida et al. 1990), but are not described as adult and socially mature until around 15 years (Boesch & Boesch-Achermann 2000; Nishida et al. 1990).

#### **1.4 Chimpanzees in Uganda**

Chimpanzees in Uganda are presently regarded as members of the eastern subspecies *Pan troglodytes schweinfurthii*. Uganda has been described as one of the most biologically diverse countries in Africa (Howard et al. 2000). 14% of the country is made up of protected areas including 10 national parks, 10 wildlife reserves and 710 forest reserves (Howard et al. 2000). Human activities such as residence, grazing livestock or cultivating crops are not allowed in these areas, although such laws are regularly broken (Howard et al. 2000). Chimpanzee habitats within Uganda fall into all three of the above categories, as well as existing in areas outside protected parks and reserves.

The population estimates for 25 forest areas surveyed between 1999 and 2002 indicate that there are around 4,500 nest-building chimpanzees in Uganda (Plumptre et al. 2003). These recent surveys, of chimpanzees and large mammals, have revealed that the greatest numbers of chimpanzees in Uganda occur in Kibale



National Park (1,300 chimpanzees), Budongo and Bugoma Forest Reserves (570 – 580 chimpanzees in each), Ruwenzori National Park (450 chimpanzees) and Kasyoha-Kitomi Forest Reserve (370 chimpanzees) (Plumptre et al. 2001; Plumptre et al. 1999; Plumptre et al. 2003). The highest densities of chimpanzees were recorded in Wambabya Forest Reserve (3.62/km<sup>2</sup>), Kibale National Park (2.32/km<sup>2</sup>), Bugoma Forest Reserve (1.90/km<sup>2</sup>), Kalinzu Forest Reserve (1.55/km<sup>2</sup>), and Budongo Forest Reserve (1.36/km<sup>2</sup>) (Plumptre et al. 2003).

#### **1.4.1 Budongo Forest, Uganda**

The Budongo Forest Reserve, the study site for this research, lies in the west of Uganda between the latitudes of 1°37' and 2°00' N, and between the longitudes 31°22' and 31°46' E (Plumptre 1996). The ground is undulating with an average altitude of about 1100m (3600ft) (Eggeling 1947). The Budongo Forest Reserve covers an area of 793km<sup>2</sup> of both moist semi-deciduous forest and grassland; 428km<sup>2</sup> of the area is forested (Howard 1991). The ecology of this forest is detailed in an extensive study by W.J.Eggling (Eggeling 1947) and described in more detail in Chapter 3. Five species of diurnal primates are found in Budongo (for more detail see Chapter 3), including the eastern subspecies of common chimpanzees, *Pan troglodytes schweinfurthii*.

### **1.5 Threats to chimpanzees**

#### **1.5.1 Africa**

Chimpanzees are classified as an endangered species throughout their range (Oates 1996). Major threats to their survival include habitat destruction and alteration, poaching (both accidental snaring and for the bushmeat trade), transmission of human diseases, and political instability. Background factors that contribute to the above threats include the increase in the human population, tourism activities, human-chimpanzee conflicts (for example crop-raiding), lack of education programs, legislation (both existent and nonexistent), habituation, lack of scientific research and lack of funding.

Habitat destruction through timber extraction, logging operations, mining, farming and other forms of land development has one of the most direct effects on the survival of forest dependent species such as chimpanzees. Total annual reduction of habitat between 1990 and 1995, in 20 of the 21 countries with remaining chimpanzee populations, was 2,701,000 hectares per year (FAO 1999). Habitat destruction leads to both habitat loss and forest fragmentation. Fragmentation creates smaller and more isolated areas, which can have huge detrimental impacts on chimpanzee populations through restricted gene flow and increased vulnerability to other pressures. Five of the 21 countries where chimpanzees exist have populations where local extinction can be expected soon, and in five more countries the resident populations of chimpanzees are so small and dispersed that they are severely at risk (Teleki 1989). Even in the 10 countries where there are more than 1,000 chimpanzees, their ranges have reduced dramatically since the 1950's (Teleki 1989). In all 21 countries the number of chimpanzees are decreasing, as the human population increases.

Poaching and hunting of chimpanzees is a serious problem throughout their range. In western and central Africa chimpanzees and other nonhuman primates are regularly hunted for the bushmeat trade. It has recently been stated that "the commercialisation of the bushmeat trade has (now) reached crisis level and represents a real risk to the survival of our closest relatives in most parts of Central Africa" (Ammann 2001, p.71). The loss of forest primates in west and central Africa to the bushmeat trade is having devastating effects on the numbers of primates surviving in these areas. There is a direct link between logging and the increase of the amount of hunting that occurs in a forest (Ammann 2001; Wilkie et al. 1992). Logging opens up otherwise remote forest areas with roads and vehicle access, logging trucks transport hunters and meat in and out of the forest, and the steel cables used in logging operations can be used to make illegal snares (Ammann 2001; Wilkie et al. 1992). Oates (1996) believes that although complete removal of a primate's natural habitat is clearly the most serious long-term threat, human predation tends to have a larger negative impact on primate populations than does selective logging or low-intensity bush fallow agriculture. He also states that the combination of logging and hunting is a growing problem in previously



remote areas of the equatorial forest region, with logging operations opening up these areas to hunters, as previously suggested (Oates 1996).

The prevention of disease transmission from humans to wild chimpanzees is of huge importance to the conservation of the species. Wallis and Lee (1999) state that: "the assurance of good health and longevity in wild primate populations is paramount to the more traditional conservation issues of poaching control and forest protection" (Wallis & Lee 1999, p.803). Types of infectious diseases that have been transmitted between humans and chimpanzees include ebola, polio, types of respiratory diseases, yaws, *Strongyloides* spp., and skin diseases (Edroma et al. 1997). At Gombe National Park, Tanzania, there are instances where infectious diseases have caused deaths and sickness in wild chimpanzees; the most likely origin was from neighbouring human populations, tourists, or from chimpanzee researchers (Wallis & Lee 1999). For example during the rainy season of 1996 an outbreak of a respiratory illness occurred in the Mitumba community, when eleven chimpanzees died. Chimpanzees have a particularly high susceptibility for human respiratory diseases, and the quick spread of this type of disease amongst a community of chimpanzees can affect many individuals at once (Wallis & Lee 1999).

Political instability is a major issue in many African countries. Breakdown of law and order leads to environmental degradation including illegal removal of firewood and trees, clearing for agriculture and increased hunting owing to lack of patrols. Political instability can also lead to loss of revenues from tourism and donors (Edroma et al. 1997). Rebels often hide out in forests, using the forest resources, and potentially causing war in those areas.

The pressure of an ever-increasing human population throughout Africa fuels all these issues. For example, in Uganda the human population tripled in the 43 years between 1948 and 1991 (4.9 to 16.7 million) (NEMA 1999), then by mid-2002 the population was 24.7 million, a number which is expected to almost double by 2025 (Population Reference Bureau – World Population Data Sheet, 2002). The population growth, on average, in the 21 African countries containing chimpanzees was 3.1% between the years of 1995 and 2000 (FAO 1999).



### 1.5.2 Uganda

Major threats to Uganda's chimpanzee population are generally the same as those for chimpanzees throughout Africa, including habitat destruction or alteration, poaching (mostly in the form of accidental snaring), transmission of human diseases and political instability. Other factors contributing to the risk of population extinction in Uganda are the tendency for chimpanzees to occur at lower densities than other large mammals (Plumptre et al. 1999), and because chimpanzee populations are spread out in isolated forest blocks, with very little chance of natural exchange between the forest areas (Edroma et al. 1997).

As described above, the bush meat trade in apes is rife throughout central and western Africa. In Uganda the situation is different. Firstly, for most people it is traditionally considered unacceptable to eat primate meat (Johnson 1996), so chimpanzees are not deliberately hunted. Secondly, hunting any vertebrate species in forest reserves is against the law in Uganda (Howard 1991). Despite this, illegal hunting does operate targeting species such as bushbuck, bush pigs and duiker. Chimpanzees and other terrestrial primates are commonly caught in snares and traps, regardless of the fact that they are not the target species (see Figure 1.1). For this reason snaring and trapping of chimpanzees in Uganda is often referred to as 'accidental'. An alarming proportion of chimpanzees are snared, and many suffer debilitating injuries including the twisting and paralysis of digits or the loss of hands or feet (see Figures 2.3 to 2.7). At least 20% of chimpanzees, at five study sites in Uganda, have debilitating injuries (see Table 2.1). Nine chimpanzees from the study community, in Budongo Forest Reserve, have injuries from snares. Chimpanzees also die from snare and trap injuries (Boesch & Boesch-Achermann 2000; Munn & Kalema 1999-2000; Wrangham & Mugume 2000).

**Figure 1.1** Adult male chimpanzee of the Sonso community with wire snare attached around fingers, first seen with snare 19<sup>th</sup> September 2000 (photograph by J.Wallis).



#### **1.6 Previous fieldwork on snaring, and the behavioural effects of injuries in chimpanzees, in the Budongo Forest, Uganda**

Hunting in the Budongo Forest has been studied as part of a research project aimed at determining the use of forest products by the human population living in the Nyabyeya Parish at the southern edge of the Budongo Forest (Johnson 1996). It was found that nearly one fifth of the people interviewed admitted to hunting, although this was probably an underestimate since hunting in a forest reserve is illegal, and so a certain amount of information might be withheld. Interestingly it was found that different ethnic groups had different views on the hunting of primates in the forest. The ethnic group native to the area say it is unacceptable to eat primates, whereas around one third of migrants from DRC that were living in the area, admitted to regularly eating primate meat (although it was not mentioned if this included chimpanzees) (Johnson 1996).

Chimpanzees that are victims of snaring in Uganda are often inflicted with life-long injuries. The injured chimpanzees of the Sonso community in Budongo Forest have been the subjects of a number of behavioural studies on the effects of these injuries.

Two studies have looked at the effects of snare injuries on feeding in Budongo. Most recently is Stokes' (1999, 2001) study on the feeding skills and the effect of injury. It was found that injured chimpanzees spent more time feeding on figs, which maximises nutrient and energy intake while minimising processing costs. They are also more likely to use a seated posture while feeding, as well as preferring to use the upper part of the tree, or any part where additional branches allow for extra support (Stokes 1999). The study also looked at the feeding techniques of able-bodied chimpanzees and the manner of compensation in the case of injury. For one food type examined (the leaves of *Broussonettia papyrifera*), able-bodied individuals showed a preference for two feeding techniques (each technique has multiple stages), while injured chimpanzees showed a preference for one particular technique. Injured chimpanzees compensated by modifying particular steps in the technique to work around their impairments, rather than inventing novel techniques. The nature and extent of the injury determined the degree of difference from the able-bodied population (Stokes 1999), and the most severely injured individuals showed reduced feeding efficiency for some food types (Stokes & Byrne 2001).

Smith (1995) looked at the effects of injuries on feeding in one species of fig tree, *Ficus sur*. His study found that injured chimpanzees increased their feeding rate in *Ficus sur* trees by using a different wadging strategy. Chimpanzees with injuries were significantly less likely to wadge for a full two-minute time period; instead they continued to pick fruit and add it to their wadge. Even with a slower picking rate injured chimpanzees were able to process the same number of figs overall (Smith 1995). Smith (1995) also found that injured chimpanzees were restricted to certain parts of the *Ficus sur* tree where the clumps of fruit were positioned amongst branches, so that they were able to lean on these branches for balance.



In a study on nesting behaviour, it was found that injured chimpanzees were twice as likely to re-use night nests when compared to those with both hands available for building nests (Plumptre & Reynolds 1997).

Quiatt and Reynolds (1994) looked at the composition of feeding groups in the Budongo Forest during the rainy season, focusing on the social integration of disabled individuals. They found that there was no significant difference for the representation of injured versus non-injured individuals, and suggested that this represents the social integration of disabled individuals in the group (Quiatt & Reynolds 1994). They also looked at the close associations of individuals, and suggested that the distance between individuals provides a rough measure of mutual tolerance and respect (Quiatt et al. 1994). They looked at disabled individuals in terms of presence in sub-groupings such as arboreal and terrestrial, and found that injured individuals were equally likely to climb into trees as uninjured individuals (Quiatt et al. 1994). They also point out that “able and disabled chimpanzees alike reveal individual differences in temperament, some shy and retiring, others are popular as grooming companions, reproductive partners, or feeding neighbours” (Quiatt et al. 1994, p.7). Data were collected for a period of only two months, which is a limiting factor in this study.

Quiatt (1996) completed a follow up to the above study on social integration and discussed the accommodations to disabilities in the Sonso community at Budongo. He suggested that the main questions that need to be addressed about the concerns of injuries on individuals included the effects on locomotion (arboreal and terrestrial), feeding (arboreal and terrestrial), social and reproductive behaviour, and disadvantages in competing for local resources and possibly selection. He discussed the concept of individual differences (as above) and suggested that individuals differ also in feeding and locomotor habits, as well as injured individuals differing in the type of injury, and the extent of the handicap imposed on the individual's behaviour by that injury, as well as the accommodations that these individuals have learnt to make (Quiatt 1996). In order to determine some of these differences Quiatt used a video camera in the field to observe injured individuals engaging in arboreal activities. Hind limb disabilities seemed to have a

greater impact on arboreal locomotion; such individuals were described as moving slowly and awkwardly in the trees (Quiatt 1996).

## **1.7 Research interest**

### **1.7.1 Behavioural effects of snare injuries**

Outside of the Budongo Forest, the effect of injuries on the behaviour of common chimpanzees has not been studied: a study focusing on some aspects of the behaviour of pygmy chimpanzees with physical abnormalities has however been completed (Kano 1984) and is discussed in section 2.2.5.1. While the effects of snare injuries on feeding have been well studied for the chimpanzees of the Sonso community in Budongo Forest, aspects of social behaviour and locomotion have been the subjects of only short-term studies. This thesis will address some of the questions outlined by Quiatt (1996), specifically the effects of injuries on locomotion and social behaviour. It will also follow up some of the ideas raised by Quiatt and Reynolds (1994), particularly the social integration of injured chimpanzees in the community. I also include in this study the effects of injury on mother-infant behaviour.

Injury is the term used throughout this thesis to describe the physical abnormalities shown by one quarter of the Sonso community of chimpanzees. One of these 'injuries' is in fact a congenital deformity, which is described in more detail in Chapter 2. This individual is included in the study alongside the snare-injured individuals, although she will be discussed separately in Chapter 8.

That so many chimpanzees in the Sonso community have survived for many years with their injuries means they must adapt well. On first observation injured chimpanzees do seem to cope reasonably well with their disabilities (personal observation). Quiatt (1996) describes individuals with injuries to hands involved in grooming interactions, feeding behaviour and in arboreal locomotion, and although modified techniques were used, by all accounts the individuals were very capable of their actions. That chimpanzees adapt so well to their injuries is possibly the reason why the effects of the injuries have gone unstudied for such a



long time. Injured chimpanzees appear to be well accepted into the community and they appear to continue to feed and groom and socialise – with some obvious adaptations to their behaviour. This study will determine in more detail if in fact injured chimpanzees are handicapped by their injuries, and to what extent. It is important to determine what impact snare injuries are having on wild chimpanzee populations, and how these effects may change with number and type of injuries sustained.

### **1.7.2 Conservation implications**

It has already been documented that chimpanzees are being killed because of accidental snaring (Boesch & Boesch-Achermann 2000; Munn & Kalema 1999-2000; Wrangham & Mugume 2000), it can then be inferred that the unintentional hunting of primates in Uganda is posing yet another serious threat to the survival of chimpanzees. I also think that for the conservation of chimpanzees in Uganda it is important to address the possibility that snare injuries can affect the behaviour of chimpanzees to the point that they have reduced social opportunities, which could in turn have implications for the long-term reproductive success of an individual. For example, one juvenile female in the study community has two injuries from snares: she is missing one whole hand and has a snare tightly caught around one ankle. Will this young female migrate to a neighbouring community, despite her obvious difficulties in travelling and in other behaviours? The welfare of individual chimpanzees should also be of concern regardless of whether disabilities can be linked to a reduction in social opportunities, or the possible long-term effect on reproductive success. If chimpanzees are handicapped either physically or socially by snare injuries, then all efforts should be made to reduce, or better still eliminate, this risk of injury and death.

As long as hunting continues in Ugandan forests, chimpanzees with one injury are at risk of a second or even third injury, which may further reduce their ability to survive and to reproduce. Three of the injured chimpanzees of the Sonso community in Budongo Forest have more than one snare inflicted injury (personal observation). It is indeed necessary to determine to what degree injured chimpanzees are disabled, and how the number of injuries impacts that level of



disability. It is also important to remember that, as the human populations increase, so too does the demand on forest products and space. One can only assume that the rate of snaring will increase as the human population increases - perhaps it is at an unsustainable level already. Unless action is taken, the issue of 'accidental snaring', the resulting deaths, and the implications that snaring has on the behaviour of those chimpanzees who remain maimed for life, will continue.

## **1.8 Aims of the research**

- To determine the effect injury has on the social grouping, maternal behaviour, grooming behaviour and locomotion of adult female chimpanzees from the Sonso community, Budongo Forest Uganda.
- To determine whether the number or extent of injuries alters the effect that injury has on the behaviour of the individual.
- To discuss ways to reduce the level of snaring in Ugandan forests.

## **1.9 Chapter Outline**

This study aims to determine how injuries affect chimpanzee behaviour focusing on: social grouping (Chapter 4), mother-infant behaviour (Chapter 5), grooming behaviour (Chapter 6) and locomotion (Chapter 7). Chapter 2 will review the available literature on snares and injuries, as well as describing in more detail the injured chimpanzees of the study community. Chapter 3 gives details of the study site, as well as describes the methods used in this study. Chapter 8 is the final discussion and conclusions, which also includes recommendations for future work and for the reduction of snare induced injuries and deaths.

## Chapter Two

### Chimpanzees, and other nonhuman primates, with injuries

#### 2.1 Introduction

The main focus of this thesis is examining the effects of injuries on the behaviour of chimpanzees. The study community, the Sonso community of Budongo Forest, Uganda, contains 49 individuals, of whom ten have serious injuries. One of these injuries is a congenital deformity, and the other nine are as a result of snare<sup>1</sup> injuries (Waller 1995). As has been mentioned in Chapter 1, the snare injuries are the result of 'accidental' snaring, as chimpanzees are not the target species being hunted. Hunting of wildlife in all Ugandan forest reserves is illegal (Howard 1991), but is commonly practised. Chimpanzees avoid a part in the local bushmeat trade only because most Ugandans do not eat primate meat (Johnson 1996). Methods that hunters use include the setting of both snares and traps. Wire nooses and spring snares are commonly used in the Budongo Forest. These are methods where a small length of wire or cord is looped and placed over a small hand built pit, and camouflaged with forest litter, for the purpose of catching terrestrial forest quadrupeds. Once a chimpanzee or other animal steps into the snare it pulls hard against the loop, which tightens and deeply embeds into the limb of the animal. The loop is either attached to a bent over sapling (see Figure 2.1), or is secured by upright branches (Waller 1995). Steel jaw traps (or man-traps) are less commonly used. The victim places weight on a metal plate that springs two parallel jaws together with great force, firmly trapping the limb (see Figure 2.2). The force of the steel jaws is great enough to sever the limb completely (Waller 1995).

Injuries are not unique to chimpanzees, or only to the chimpanzees of the Ugandan forests. Nonhuman primates, throughout their ranges, are exposed to the dangers of injury to limbs whether by accident (i.e. falling from a tree), disease, predation, or through an aggressive interaction or from being caught in a hunter's

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<sup>1</sup> the term "snare" is used throughout the text to describe all trapping methods including spring snares, wire nooses and steel jaw traps, except where otherwise stated.

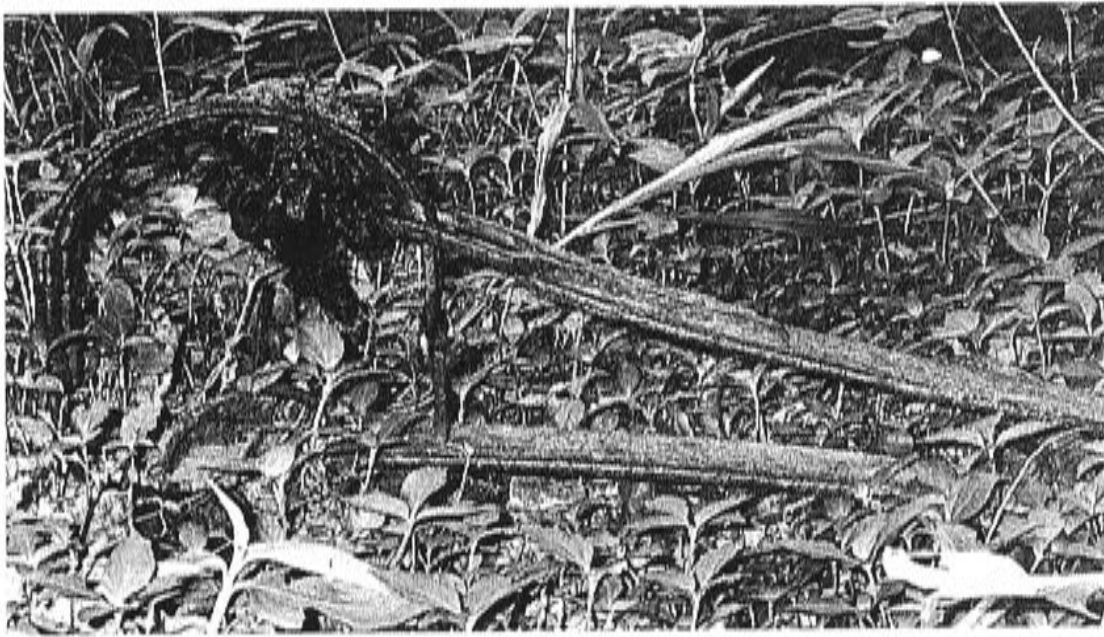


**Figure 2.1** Wire noose snare, Budongo Forest. This wire noose is camouflaged by leaf litter, the wire loops in a circle on the ground on top of the layer of sticks. An animal places a foot or hand in the loop, falls down the hole dug under the sticks, then the sapling springs, tightening the noose around the limb.



snare. Limb defects are also caused by congenital deformities. These injuries, regardless of their cause, will have impacts on various aspects of an individual's behaviour. Injured primates have been recorded at many different sites, and in some cases their behaviour has also been recorded. These studies will be discussed at length in this chapter.

**Figure 2.2** Steel jaw trap, Kasokwa Forest Reserve, Uganda. The hand of a chimpanzee is still caught in the metal jaws.



## **2.2 Injuries and their effects on nonhuman primates**

### **2.2.1 Japanese macaques**

A particularly striking example of behaviour associated with injuries comes from Japanese macaques (*Macaca fuscata*). The Japanese macaque lives from Shimokita peninsula in the north to Yakushima Island in the south in a diversity of habitat, from sub-tropical forest in the lowlands to sub-alpine forest in the mountains (Nakagawa et al. 1996). Congenital malformations of the limbs have been observed over a wide part of the Japanese macaque range since the 1950s (Nakamichi et al. 1997). One particular group, the Awajishima group (a free-ranging, provision fed group on Awajishima Island, in the eastern part of the Seto inland sea) has a higher than usual annual average rate of births of malformed infants, as much as 25.0% for the period between 1969 and 1980 compared to 4.2% for other Japanese macaque groups between 1952 and 1978 (Nakamichi et al. 1983a, b).

Studies have been conducted on the behavioural development of these infants with malformations. A malformed male, completely lacking both hands, was observed for a period of four years from his birth (Nakamichi et al. 1983b). The infant was unable to cling to his mother or reach her nipples without being supported. As he



grew older he developed a unique locomotor pattern of bipedal walking, and he was unable to climb well. No social disadvantages based on his malformation were observed; he maintained a stronger bond with his mother than other male monkeys of the same age and retained the same high rank as his mother (Nakamichi et al. 1983b). A second malformed infant, that was observed for only one year, showed the same behavioural development as the first infant described. In addition, self grooming and scratching were difficult and usually involved rubbing body parts with his stumps of hands or rubbing against trees or stones. Social interactions were affected; the malformed infant developed relations with adults, rather than same age infants and older juveniles. Play intervals remained at 5% for the whole of this malformed infant's first year, whereas normal infants increased their level of play to 20% in the first 12 months (Nakamichi et al. 1983a).

A third example is from a different population of Japanese macaques living in Jigokudani Monkey Park, near Nagano. The park is home to more than 200 macaques and is part of the Japanese Alps. Hot pools act as temporary escapes from the cold, and provision feeding makes life easier for them. One particular macaque, Mozu, is well known as she lacks both hands and feet. She is only able to crawl over the ground, and is unable to escape into trees to avoid the ice and snow. Despite her almost useless arms and legs, Mozu successfully raised five offspring, none of whom had her abnormalities (de Waal 1996). In 1991 the group of macaques that Mozu belonged to split in half. Mozu originally went with the lower ranking group, being of a low rank herself. The dominant group took over the feeding area, and Mozu then began joining this group despite ties to her offspring in the low ranking group (female macaques normally maintain lifelong bonds of kinship). After time, and many attempts to groom (despite not having any fingers), and occasional attacks, she was eventually accepted into the group (de Waal 1996).

These three examples of Japanese macaques with extreme malformations show how behaviour can be altered for survival within a troop.



### 2.2.2 Gibbons

Another example of how injuries can affect primate behaviour is described for a female gibbon (*Hylobates lar*) from KhaoYai National Park, Thailand. Her arm appeared to be broken (although no proof was available) and could not be used for two months (U.Reichard, personal communication). Her group was observed to wait for her, as her movements were very slow. The injured female also entered her night tree earlier, and started the day range later than other group members. The rest of the group seemed to pick up the pattern of entering night trees earlier, although they did not start the daily activity much later, rather they just spent time nearby until the injured female left her night tree and started foraging (U. Reichard, personal communication).

### 2.2.3 Mountain gorillas

Mountain gorillas (*Gorilla beringei*) are commonly victims of poachers' snares. They live on the Virunga Volcanoes on the DRC-Rwanda-Uganda border (Schaller 1963). As in Uganda, snares are set in the forest in an attempt to catch duikers and bushbuck. The gorillas are unintentional victims and can be both maimed and killed from these encounters. In a recent publication, injuries to mountain gorillas by poachers were compiled from the years between 1971 and 1998. 67 accounts of poacher induced injuries were recorded, of which 75% were from snares (four of these individuals died), 9% were by firearms, 7% were by spear and arrow and 9% were from unknown causes (Mudakikwa et al. 2001).

Some examples of these injuries were recorded by Fossey (1985). She observed three gorillas, on separate occasions, which had become caught by wire snares around a wrist. They all used feet instead of hands for processing food items and became noticeably weaker over time, eventually disappearing from their groups and not seen again (Fossey 1985). Another case was a young female from Karisoke who was observed continuously throughout her short life. She received a snare that was attached tightly just above her ankle. She lived for sixty days during which her foot became gangrenous. The group slowed down their travelling speed so that the disabled gorilla could keep up with them. Although

treatment was given, it came too late and she died of both gangrene and pneumonia (Fossey 1981, 1985). Two further cases that are described by Fossey (1985) include juvenile gorillas that were snared around the wrist. In both cases the silverback leader of the group was responsible for removing the snare using his canines (Fossey 1985). And yet another individual, an adult female, was missing some of the fingers from both hands when first seen as an adult, and was most likely a snare victim. She was observed with an infant and was able to care for that infant extremely well despite her injuries (Fossey 1985).

In a study relating to feeding skills in mountain gorillas it was found that an adult female who had injuries to both hands had no reduction in food processing efficiency when compared to non-injured female gorillas (Byrne & Byrne 1991).

Mountain Gorillas are still under threat from snares. A Field News Article written for the Dian Fossey Gorilla Fund describes the recent snaring of a young female (Williamson 2000). It also states that daily anti-poaching patrols destroy snares and the Karisoke staff collect and burn around 1000 snares a year (Williamson 2000).

#### **2.2.4 Lowland gorillas**

Less is known about injuries, especially from snares, in the case of lowland gorillas (*Gorilla gorilla*). Their habitat extends through southeast Nigeria, Cameroon, Rio Muni, Gabon and Congo (Brazzaville) (Groves 2001). An early report tells of one adult male lowland gorilla that was observed with an injury, although it does not state the cause of the injury. Despite having most of his right arm missing, this male was still the leader of his group (Schaller 1963). Also mentioned are two gorillas, one with a deformed leg and the other with a deformed foot, but the cause of these injuries is not given.

## **2.2.5 Chimpanzees**

### **2.2.5.1 Chimpanzees outside Uganda**

#### **Taï National Park, Côte d'Ivoire**

The Taï chimpanzee project is run in the Taï National Park in the southwest corner of Côte d'Ivoire, West Africa. The habitat is almost all undisturbed primary rainforest. 123 community members have been identified, of which nine have been observed with swelling associated with a hand or a foot caught in a snare, and one juvenile is known to have died from a gangrenous snare wound (Boesch & Boesch-Achermann 2000). As with other sites, local hunters accidentally snare chimpanzees; in this case the range of the chimpanzee community has one of its borders along the edge of the forest with fields and villages not too far away. There are many remarkable examples from the Taï Forest where chimpanzees have been freed from snares. One such example is of a young female who had her left wrist caught in a snare trap. "Spinning wildly on the ground she was able to break the cable but not to remove the snare that was by then cutting deep into her flesh. Rapidly, Schubert, the beta male, approached, and while she held her arm towards him, he removed the cable with his canine" (Boesch & Boesch-Achermann 2000, p.251). Other occasions are also described. For example an adult male freed himself from a snare attached to his left wrist leaving his inner arm injured, and a second male was snared around his right ankle and was able to break the cable rapidly and remove the snare 7 days later without any lasting injury (Boesch & Boesch-Achermann 2000). Yet another male dragged a snare for six weeks. On this occasion the snare was made from very thin wire and would have been difficult to remove. There is also a case of a very young infant becoming caught in a snare that the mother presumably removed (Boesch & Boesch-Achermann 2000). Juveniles were found to be incapable of removing the snares; of the five juveniles with a cable embedded into the flesh, four kept it on for between eight and 11 months and were badly handicapped as a result, while the fifth died (Boesch & Boesch-Achermann 2000).



### **Gombe National Park, Tanzania**

The Kasakela community of chimpanzees live in the Gombe National Park, Tanzania. During 1966 there was an outbreak of a paralytic disease in Gombe, with twelve individuals affected by the disease: three died, two were destroyed as they were so badly affected, and six others were crippled (Goodall 1968). Two mature males that each had a paralysed arm, adapted by walking long distances in a bipedal position, and after two or three months they were able to keep up with the other group members. When these two males became crippled, their loss of status was immediate and very obvious, but after they adapted to their paralysis they began to rise in the social ladder once more (Goodall 1986). The other crippled individuals were seen to gain some movement in their affected areas, and seemed to adapt well to their paralysis (Goodall 1968).

Bygott (1979) also gives an example of how illness can affect status. One individual, who was the alpha male until 1964 and remained high ranking until 1968, lost his rank very quickly when he suffered a period of illness; he then became one of the lowest ranking group members (Bygott 1979).

Another individual at Gombe was born with a deformed right foot, probably a clubbed foot. She was described as sometimes having difficulty in keeping up with a fast-moving party of adults because of her lameness (Goodall 1986).

### **Mahale Mountains National Park, Tanzania**

Aside from minor injuries associated with fighting, no other injury type is recorded for the chimpanzees at Mahale. The only mention of the number of defects in limbs is a personal communication to T. Kano by T. Nishida in Kano's (1984) paper on injuries in bonobos. It is stated that "common chimpanzees of Mahale have a far lower frequency of defects in limbs than bonobos of Wamba" (Kano 1984, p.10).

## **Wamba, Zaire**

Kano (1984) conducted a study on bonobos (*Pan paniscus*) at Wamba, DRC. Hunting using snares (but not targeting bonobos) is common at Wamba, and two cases of bonobos seen foraging with a wire from a snare embedded tightly around a limb have been observed. The study looked at individuals from two groups, of which nearly half had some kind of physical abnormality to the limbs (Kano 1984). Despite being unable to determine the exact cause of the deformities, he described the degree of influence the deformities had on the bonobos' survival. Most affected individuals showed differences in use of locomotion, although they were all still quite active and agile in the trees and on the ground. One severely injured individual (two stiff legs) was extremely affected by his injuries, moving very slowly and using "crutching" both in the trees and on the ground, yet he was still able to climb to the top of the tallest trees to forage. This same individual did not exhibit any dominance behaviour toward any of his group members. No other injured individuals showed signs that their rank had been affected by their injuries, and all five of the highest ranked males of one of the groups had hand, foot or digital abnormalities. In bonobo society it is suggested that age is the principle factor affecting social status, and social position is more important than small differences in locomotor ability in gaining access to food (Kano 1984).

### **2.2.5.2 Chimpanzees in Uganda**

#### **Kibale National Park**

##### **Kanyanchu**

Kanyanchu Tourist Centre is located in the Kibale National Park, west Uganda. The Kibale Primate Habituation Project has been working from this site, habituating the Kanyantale community of chimpanzees and other nonhuman primates in the forest. The project started in 1997 and has been continuing since that time. Forty-six chimpanzees (over 6 years of age) have been identified and named, but this not the whole of the community. Ten of these individuals (22%)

have snare injuries (see Table 2.1), and another three have missing digits or half digits. These may be snare injuries but it is also possible that they were bitten off.

**Table 2.1**      The percentage of chimpanzees at five study sites in Uganda with known or suspected snare related injuries

<i>Study Site</i>	<i>Percentage</i>	<i>Source</i>
Budongo (Sonso)	25% (Sept, 2000) *	Waller & Reynolds, 2001; J.M., pers.obs.
Kibale (Kanyawara)	27% (from 1988-1999) *	Wrangham and Mugume, 2000
Kibale (Kanyanchu)	22% (Oct, 2000) **	J. Lloyd, pers.comm
Kalinzu	56% (1998) #	Hashimoto, 1999
Kasokwa	50% (Feb, 2000) #	Lloyd & Mugume, 2000

\* individuals in community aged 6 years or above, defined as a “snareable” age (Wrangham and Mugume, 2000) – whole community is known

\*\* individuals in community aged 6 years or above – identified individuals in community only

# identifiable individuals in community only

### Kanyawara

The Kanyawara chimpanzee community is in the northwest part of Kibale National Park; the community averages around 50 individuals (Wrangham & Mugume 2000). Out of the 59 “snareable” chimpanzees (those six or more years old) observed at Kanyawara, four have lost a hand and 12 have wounds such as loss of knuckles, bent wrists and crippled feet; a total of 27% (see Table 2.1) (Wrangham & Mugume 2000). It has been observed that the Kanyawara chimpanzees do sometimes recognise a concealed snare and avoid it, although obviously this is not always the case, as there have been 15 known fresh snare wounds in the 13 years since the Kibale Chimpanzee Project began (Wrangham & Mugume 2000).



One Kanyawara chimpanzee has died from a snare wound (Wrangham & Mugume 2000), which is described in the following example. A juvenile female, around 9 years old, lost her left hand at the wrist to a snare in 1995. She received a further snare injury to her right hand in 1998; the snare wrapped around all four fingers below the knuckles. Both moving and feeding were difficult for this juvenile. A month later her mother was found dead from a respiratory illness, and the juvenile female was left with a two-year-old brother to look after. Both individuals disappeared, first the infant male, and then the juvenile female (Muller 2000).

In 1997 a snare removal project was initiated to remove snares from the Kanyawara area of the Kibale National Park. The total number of snares removed by two persons from the beginning of the program until June 2000 was 2290, an average of 67 snares per month, which suggests that 15000 snares are present at any one time in the 760km<sup>2</sup> National Park (Wrangham & Mugume 2000). There was a seasonal difference in the probability of finding snares and the number of injuries recorded. It appeared that fewer snares are set in the dry season, and most are set in the weeks during and just after rainy periods.

### **Ngogo**

Ngogo is located 10km southeast of Kanyawara. When Kibale Forest was gazetted as a forest reserve, Ngogo was set aside as a small nature reserve. Two individuals have been observed with injuries that were thought to be a result of snaring. One adult male and a young adult female both had a healed over stump from which a hand had been amputated (Ghiglieri 1984). Ghiglieri also described a young juvenile from Kanyawara with a hugely swollen and gangrenous left foot, with the wire snare still tightly wrapped around the ankle (Ghiglieri 1988). Recent data on snare injuries at Ngogo is unavailable and so has not been included in Table 2.1.

### **Kalinzu**

The Kalinzu Forest Reserve is located in southwestern Uganda and is classified as a medium altitude moist evergreen forest. Chimpanzees, and five other species of

diurnal primates, inhabit this forest. One community of chimpanzees lives around the sawmill that is in the western part of the Kalinzu Forest, and this community has been habituated since 1997 (Hashimoto 1999). 16 adult male chimpanzees have been identified (which is thought to be most of the community's males), and a few adult females and immature individuals have been identified. Of these individuals, nine have injuries with a high probability of being caused by snares (Hashimoto 1999) (see Table 2.1). Two of the males still had the wire embedded in their wrists, two males had complete loss of a hand or foot, one female had a paralysed hand with hair loss and another male had a clawed hand. Five other individuals had injuries that may be attributed to leprosy, but also may be caused by snares, such as loss of digits, hair loss around the ankle and paralysed fingers. Hashimoto (1999) suggests that as these individuals showed no other signs of leprosy, the afflictions were most probably caused by snares.

### **Semliki**

The Semliki Wildlife Reserve is located in the west of Uganda; Lake Albert is the reserves northern boundary, and the Ruwenzori Mountains its southern boundary. Although snares have been found in the reserve no chimpanzees have been seen with snare related injuries (Hunt & McGrew 2002). Chimpanzees have been observed in Semliki since 1996, the progress of habituation has been steady, but slow compared to other populations. Direct observation of chimpanzees averages 3.4 hours per month for the study group, Mugiri (Hunt & McGrew 2002). As habituation of individuals in the community increases, so to may the observations of injury. Since only three individuals are identified, this community has not been included in Table 2.1.

### **Kasokwa**

Kasokwa Forest Reserve is a small isolated patch of riverine forest, roughly 1.4km<sup>2</sup>, in Kinyara District, western Uganda, near the Budongo Forest Reserve. A small group of chimpanzees lives in this depleted forest patch, and 50% of the sub-adults and adults in this group have injuries most likely to be a result of snares (Lloyd & Mugume 2000) (see Table 2.1). Snares and traps are commonly set in

this forest, and as in other areas the target species are not chimpanzees. As Kasokwa is surrounded by fields and villages, and in some parts is only a few metres wide, there is a lot of human encroachment on the forest.

It is possible that metal jaw traps are more common on this forest patch as many of the injuries are the complete severance of a limb. An injury of this type occurred during the study period, resulting in the death of an adult male chimpanzee (Munn & Kalema 1999-2000). On 6 June 2000, local people first observed 'Kigere', the alpha male chimpanzee of the Kasokwa community, dragging a large steel jaw trap on the fingers of his right hand (see Fig. 2.2). On 17 June, R. Kyamanywa (field assistant) found Kigere under bushes just outside of the Kasokwa Forest; he was dead, with the trap still on his fingers. His right leg was missing below the knee. This was probably the result of a previous snare injury. Villagers reported seeing other chimpanzees shaking mangoes from a tree, enabling Kigere to continue eating up until his death. It was also reported that he was climbing trees with the trap on his hand (Munn & Kalema 1999-2000). A recent nest he had used was found just above the ground (personal observation). Veterinarian, Gladys Kalema carried out a post-mortem examination on 18 June 2000 (assisted by author). The trap (40cm in length and weighing 10kgs) was attached across the distal metacarpals of the right hand. Based on the observations of local villagers, it is believed that the trap was attached for 10 days. As a result, the right arm developed extensive gangrene, which led to overwhelming septicaemia and toxemia<sup>2</sup> (Munn & Kalema 1999-2000).

### **Budongo Forest Reserve**

The study community is the Sonso community of chimpanzees living in the Budongo Forest Reserve. The study site is described in detail in Chapter 1 and 3 (sections 1.4.1 and 3.1). Out of the 49 individuals in the community, 36 are aged six years or above (a 'snareable' age, as defined by Wrangham and Mugume,

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<sup>2</sup> Gangrene: in a living animal, death of a part of the body sufficiently large to be seen.

Toxaemia: a term applied to forms of blood-poisoning due to the absorption of bacterial products (toxins) formed at some local site of infection.

Septicaemia: a serious form of blood-poisoning due to the multiplication in the blood of bacteria (Thompson 1984)



2000), and nine of these (25%) have injuries from snares (see Table 2.1). Three of the snared individuals have injuries to more than one limb.

A detailed account of the studies that have been conducted on the effects injury has on the chimpanzees of the Sonso community appears in Chapter One (section 1.6). Aside from these studies there have also been anecdotal observations made by field researchers. Newton-Fisher (1999) states that Tinka “who was old and crippled” was the only adult male who spent a considerable proportion of his time away from other males (Newton-Fisher 1999, p.725). Fawcett (2000) stated that Zana, who is severely handicapped, might have altered her association levels because of her injuries, and this is possibly why Zana’s juvenile son spent more time with another mother, Kwera. It was possible that Kwera took on the role of adoptive mother (Fawcett 2000). Also mentioned in Fawcett’s study was another handicapped mother, Banura; it was suggested that her old age and handicap might have affected her association patterns (Fawcett 2000).

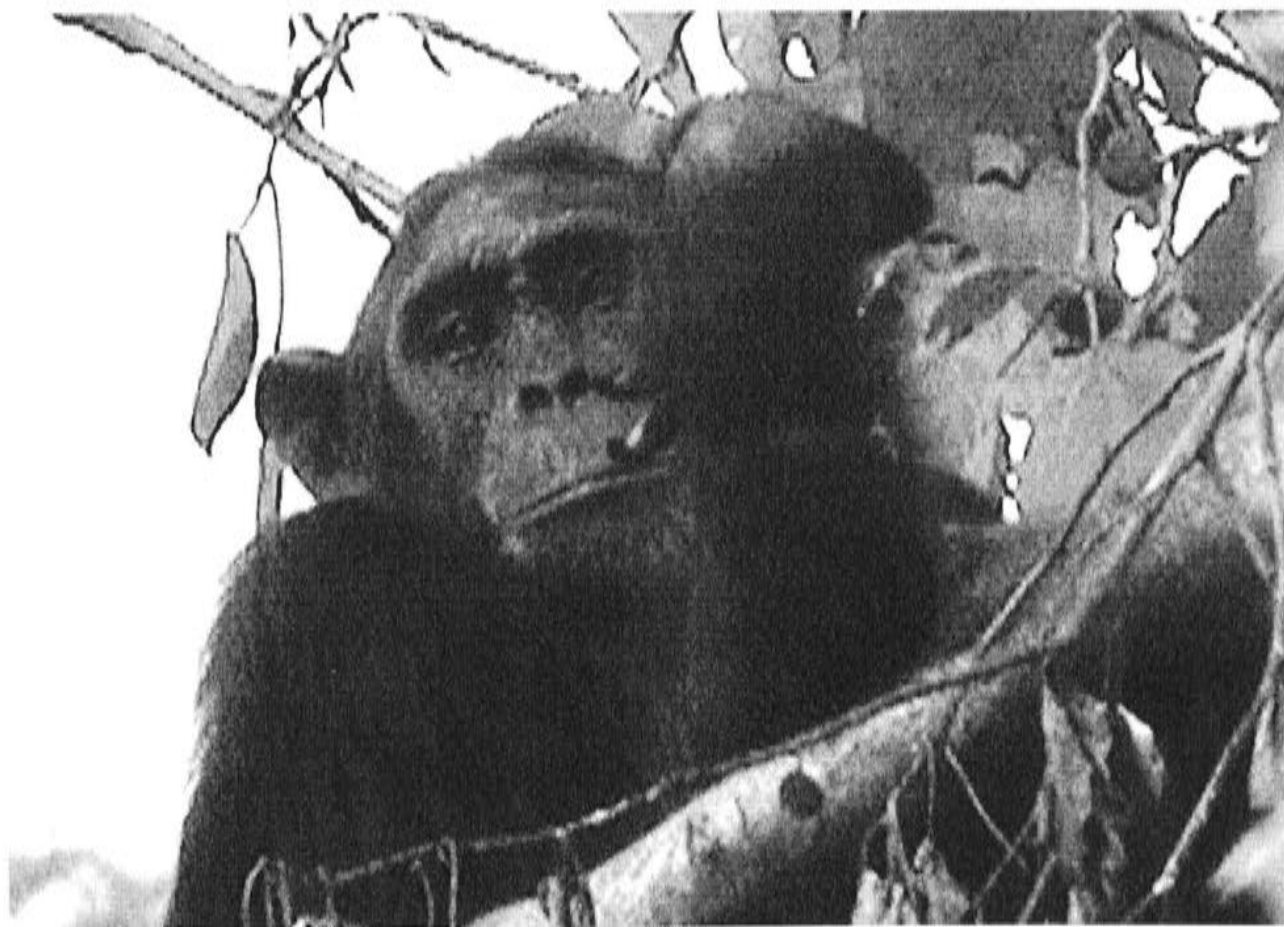
As mentioned above, the study community of chimpanzees has nine individuals with snare injuries, and a further one individual with a congenital deformity. One of the individuals was snared during the current study period; all of the other individuals have had their injuries from before the onset of this study. Below I describe in detail the injuries of the Sonso community. For the chimpanzees who were injured before the project began (1990), I refer to a study that was conducted on the Budongo chimpanzees to determine the causes of their limb deformities (Waller 1995; Waller & Reynolds 2001). In Waller’s study, field sketches and assessment charts were used to determine the involvement of particular tendons, muscles, nerves and blood vessels, and for each limb he produced a detailed picture of the configuration of the injuries in order to determine the cause. Of the 11 cases of limb abnormality observed at the time of the study, 10 were attributed to snare and trap injuries (Waller 1995). Seven of those individuals are described below. For the younger individuals that were snared after 1990 when the project commenced, the cause of the injury is definitely known, and described here based on information from the Budongo Forest Project Events Book.

### Study individuals – Adult females with dependants

Adult females with dependants were the focus of this study because at the onset of the study they were the age/sex class with the most injuries (since that time two males, plus a very young female, have been wounded seriously from snares). Only one age/sex class was chosen to study, as this greatly reduces natural variation in the data caused by behavioural differences seen between individuals.

**Kalema** has an injury resulting from a wire snare on her right hand; there are reports that she bore the remains of a wire snare on her wrist for some time after the injury (Waller 1995). Her hand is paralysed and hooked from the wrist, with the fingers bent so far forward they almost touch the inner part of the lower forearm. Her fingers are curled right over, and seem to come together at a point; they appear to have no strength or mobility (see Figure 2.3).

**Figure 2.3** **Kalema**, holding her injured hand up to her face. Note the hooked nature of the wrist, and the fingers bent back to the forearm.  
(photograph by J.Wallis)



**Kewaya's** right hand is injured from a wire snare; like Kalema, she was observed in earlier days of the project with the snare attached to her wrist (Waller 1995).

The hand is extremely deformed being both twisted and hooked (see Figure 2.4). The wrist is so twisted that the fingers of her right hand point out to the side. The fingers come together at a point (similar to Kalema). Her hand is paralysed in this position so her fingers lack any function.

**Figure 2.4**     **Kewayaya**, note the twisted wrist on the right hand, and the fingers pointing out to the side.  
(photograph by J.Wallis)



**Kigere** is missing the entire foot of her right leg. The injury is likely to have been caused by a wire snare that became gangrenous, or by a larger metal trap (Waller 1995)

Both of **Zana's** hands are injured as a result of snares (Waller 1995; Waller & Reynolds 2001). Zana's left hand resembles the injury of Kewayaya's right hand (see Figure 2.5). The wrist is twisted and the fingers are deformed, the fingers appear to point out sideways and are very floppy, seeming to lack any voluntary movement. Zana's right hand has only one finger, the forefinger, and she has the



remaining stump of her thumb (see Figure 2.5). The missing digits, or perhaps the snare itself, have caused a great weakening in the wrist (Waller 1995).

**Figure 2.5** **Zana**, the hand held above her head, to the left of the image, has the missing digits and the hand closer to the face, the left hand is deformed and twisted.  
(photograph by J.Wallis)



**Banura's** left foot is considerably enlarged (appears swollen), not capable of much movement, and has only two digits. One digit is like a small finger or thumb, and seems to have some ability to grip. The other digit is larger and folded over toward the centre of the sole of the foot.

Banura is the only individual in the Sonso community thought to have a congenital deformity (Waller 1995; Waller & Reynolds 2001). She is included in this study because she has a physical disability, and this shows signs of affecting her behaviour. The main difference between her disability and the snare wounds is that she would have been born with her deformity. Although Banura is designated as "injured" in this thesis, and included in general discussions on effects of injury, she will be discussed in a separate section in the final discussion. The focus of this study is to determine how chimpanzees cope with injuries. As ninety percent of the deformities seen in the Sonso community are directly attributable to snares,

the conservation and welfare of chimpanzees is discussed in this thesis with relation to the effects injuries have on chimpanzee behaviour.

### **Other injured individuals in the Sonso community**

**Muga** (adult male) is missing his right hand (Figure 2.6), but he still has his right wrist and is able to use the wrist joint quite freely; he uses the joint to assist in feeding, locomotion and grooming. Waller (1995) suggests that this type of injury is most likely caused from a wire snare that became gangrenous, or from a large metal trap (as for Kigere above).

**Figure 2.6** **Muga**, showing the stump of his right hand, in the bottom left hand corner of image.



**Mukwano** is a nulliparous adult female. She has a snare embedded on her right foot. The foot is slightly swollen and Mukwano limps on the foot both when travelling on the ground and in the trees. The snare was first seen on the 5<sup>th</sup> of July 1999.

**Shida** (juvenile female) is the daughter of Banura. She has two injuries, both as a result of snares. Her first injury was seen on 1<sup>st</sup> of June 1998. A deep flesh wound was seen around her left wrist, where a snare had embedded itself. The wire from the snare could be seen, but the loop could not as it was too far embedded. The hand was hanging limply down and was not used at all. The injury when first seen was no more than a week old. A few days later the hand was hanging from the wrist by only a thin piece of skin, and a month later the whole hand had been severed leaving a swollen stump (see Figure 2.7) (Budongo Forest Project Events Book, 48). Her second injury was seen less than a year later on the 25<sup>th</sup> May 1999 (Budongo Forest Project Events Book, 62). This time a cord snare was attached on her right leg around the ankle. This cord snare was still visible during the present study period (see Figure 2.7), with the right leg becoming obviously thinner. She rarely used her right leg when walking on the ground, but held it up to her chest and walked tripedally. Her left hand stump was used for balance, and in some grooming and feeding behaviours. She appeared to still have some movement in the left wrist.

**Figure 2.7** **Shida**, note missing left hand and the cord snare that is just visible on her right foot, it can be seen as a knot of cord at the back of her right ankle.





**Tinka** (adult male) is the most severely injured male in the community. He has injuries to both his hands. His right hand is the most severely deformed; the wrist is wasted and completely paralysed. The fingers are curled around and are pointing in towards the inner arm; voluntary movement is impossible, although the digits can passively extend. His left hand is also paralysed, although the wrist is still capable of some flexion and extension (perhaps 45 degrees as opposed to a normal almost 180 degrees). The hand appears hooked and the wrist is wasted; only the thumb has retained function, the fingers are all paralysed in the hooked position, the thumb is therefore of great assistance in grasping food items. Tinka often has large open wounds on the back of his hands as a result of knuckle walking using the back of both wrists as the point of contact with the ground. Waller (1995) determined that both of these injuries are a direct result of snares.

**Gershom** (sub-adult male) was snared during the study period; his injury was first observed on 2<sup>nd</sup> of March 2000 (personal observation). His right hand was swollen, with a very thin wire snare wrapped around two of his fingers. He was unable to use his right hand for movement, but was able to use it for feeding. He walked tripedally, and also began spending a large amount of time with Tinka. This may be because Tinka is also injured, or it may be that they are related (the later is unknown at present, although it was not suspected before Gershom was injured).

During the study period, on 10<sup>th</sup> of December 1999, **Maani** (adult male) was seen by one of the field assistants with a scar / injury on his left wrist. He was seen again on the 13<sup>th</sup> of December by the author. The injury looked to be approximately 1cm deep and was white in colour. It would seem likely that the injury was from a snare, which Maani had managed to escape. The injury healed well.

**Nick, Bwoba** and **Andy** (the first two are sub adult males and the third is a young adult male) all had snare injuries from which they have fully recovered (Budongo Forest Project Individual Life History Records). Both Nick and Andy had wire snares caught around their right ankles (Andy in 1994 and Nick in 1995), and Bwoba had a wire snare caught around his left wrist (in 1992).

**Grinta** (juvenile female) was the daughter of Ruhara. She was seen on the 9<sup>th</sup> of June 1999 with a wire snare on her right upper arm, between her elbow and shoulder; she has not been seen again since that day. Both her mother and younger sister, Rose, have been seen frequently. Grinta was younger than would be expected for a female to emigrate, so it is assumed that she died from the snare injury, although no skeleton was ever found (Budongo Forest Project Events Book, 62).

### **Evidence of snaring activities during study period**

During the study period evidence of snaring was seen both in the study community range, and also beyond that area in the range of neighbouring chimpanzee communities. Below are some of these events listed in chronological order:

29<sup>th</sup> of October 1999

Trail cutters, employed by the Budongo Forest Project, alerted the project to a chimpanzee thought to be caught in a snare. We visited the site, which was far enough away from the field camp that we presumed that the chimpanzee involved was from a neighbouring community. When we reached the area where the incident was recorded, no chimpanzees could be seen, but calls could be heard nearby. Despite tracking, no chimpanzees were sighted. Two wire snares, still set, were found while we were walking to the site, and a further eight snares were found in the area of the incident. Seven of these were still set; the remaining one was sprung and frayed, and appeared to be the one responsible for the snaring incident that had been reported. A temporary hunter's hut was also found near the area.

22<sup>nd</sup> of November 1999

Two snares were found in the grid system (Block J6), hence within the home range of the study community of chimpanzees. Both snares had caught black and white colobus monkeys, one was dead, the other was still alive with the snare caught around its neck. Two of the field assistants were able to cut the colobus

monkey free, as the snare was made from cord. It was assumed that the monkey had been in the snare for around three days, as there were maggots at the site of the wound, and the monkey was very weak; its survival seemed doubtful. Both snares were found approximately 10 metres from the trail.

23<sup>rd</sup> and 24<sup>th</sup> of November 1999

Old rusty wire snares were found on both days, one within the trail system and one beyond. Other researchers at the project found both snares. One was still set; the other had a small bone attached, which was most likely to be that of a duiker. Unfortunately not all snares are checked regularly by hunters, and often left for many months, either lost or forgotten.

25<sup>th</sup> of November 1999

A bushbuck was found with a snare attached around its right foot just above the fetlock joint. The snare had been broken and the bushbuck was dragging the wire, it appeared that it had been in the wire snare for at least a week (W.Boardman, personal communication). A Veterinarian removed the snare, the wound was cleaned, and fluids, antibiotics, steroids and vitamins were injected intravenously. The bushbuck was very weak, and it is unknown if it survived.

15<sup>th</sup> of December 1999

A wire snare was found in the grid system (Block 2A) very close to camp. The snare was still set, and was found while chimpanzees were being observed in trees just above it. The snare had been set about 10 metres from the trail.

10<sup>th</sup> of January 2000

A snare removal program began, focusing on the area covered by the grid system (i.e. the home range of the study community). Two local ex-hunters were employed to remove snares. In the period between 10<sup>th</sup> to the 31<sup>st</sup> of January 2000, a total of 231 snares were found and collected (Figure 2.8). The material used to make the snares was recorded (counted and sorted by the author); 23 were thick wire, 160 were thin wire, 47 were made from cord or nylon, and one was made from other material (this included things like fishing line and electrical cord). During the month of February a total of 172 snares were collected; seven were



thick wire, 147 were thin wire, 14 were cord or nylon and four were made from other materials. In March a total of 111 snares were collected; 11 were thick wire, 77 were thin wire, four were cord or nylon and 19 were made from other materials. The snare removal project was temporarily suspended at this point as research items were being taken from the forest, and it was thought that further education was needed in order for local hunters to understand the reasons for the removal of the snares.

**Figure 2.8**     Snares found in the first three months of snare removal at Budongo Forest.



### 2.3 Discussion

Injuries are widespread amongst nonhuman primates, and vary in their causes. Amazingly, individuals do survive severe injuries, such as the loss of an entire hand or foot. A human in the same situation may not fare quite so well. Waller (1995) discusses the survival of severely injured chimpanzees using the argument that the natural blood flow allows the wound to be cleaned of foreign matter, which reduces the risk of infection. He supports this argument with comparisons from human injury, where some surgeons argue that the primary suture should be

delayed for up to 3 to 5 days (Waller 1995). Stokes (1999) lists other factors contributing to the survival following injury in chimpanzees; these include the use of medicinal plants by chimpanzees (Huffman & Wrangham 1994, for example), and the change in behaviour of other community members towards the injured individual (Stokes 1999). Examples of the latter can be divided into: tolerance by other community members, and active community or individual support. A good example of tolerance from this chapter is described for high-ranking Japanese macaques that allow the extremely handicapped 'Mozu' into their group, despite her kin ties with the low ranking group. Active community or individual support can be seen in the examples discussed where chimpanzees and gorillas remove snares from victims. Behavioural adaptations to limb injuries are also important factors in allowing an injured individual to survive.

Disabled individuals have been found among hominid fossils (Frayer et al. 1987; Putman 1988; Solecki 1971). Palaeontologists have recovered a number of individuals whose remains show evidence of impairments such as dwarfism, crippled limbs and spina bifida, and these finds have "been interpreted by some writers as evidence for compassion and 'moral decency' among other members of the community" (Dettwyler 1991, p.375). Dettwyler (1991) argues that there are many assumptions in these interpretations such as non-productive members of a society being rare and presenting a major strain on that society, and that disabled members contribute nothing to a community. DeWaal (1996) argues that these fossils show nothing more than a tolerant attitude towards handicapped members, as is the case for the example given of 'Mozu' the Japanese macaque (de Waal 1996). The key to survival for injured chimpanzees may be similar to what may have been the key to survival of injured hominids of the Plio-Pleistocene; that being the free flow of information between injured and non-injured members about local resources, and communication and equal responses between all individuals (Quiatt et al. 1994). In human communities this is termed tolerance or respect (Quiatt et al. 1994). Examples of active support, such as the removal of snares from victims by gorillas and chimpanzees (see sections 2.2.3 and 2.2.5.1) may be evidence for compassion, but this behaviour has not been recorded for other communities of chimpanzees. It is unknown why individual apes in some communities have learnt to remove snares, and others have not.

It has been shown in this chapter that injuries to chimpanzees and other primates, whatever their cause, are reasonably well documented in the literature. Primates, and more specifically chimpanzees, can survive serious injuries (although not all do), they are shown tolerance from other community members, and in some cases are even shown active support by particular individuals. Examples from this chapter, and the previous chapter, suggest that once an injury is survived, primates adapt well by using behavioural modifications where necessary, although the social repercussions are varied. This study will focus on one community of chimpanzees, as described above, and will determine how they are affected by their injuries. What behavioural adaptations do they show, are other community members tolerant, and do they show any examples of active support to injured individuals? As stated at the end of the previous chapter the main aims of this study are: to examine four major aspects of the behaviour of adult female chimpanzees from the Sonso community, to determine how injury affects these behaviours, and to determine if the number or severity of injury affects the extent of any behavioural impairment. The behavioural aspects studied here are those that have been previously unstudied, or subject to only short-term studies: grouping and association patterns, mother-dependant behaviour, grooming behaviours and locomotion.



## **Chapter Three**

### **The Study Site and Methods**

The aim of this study is to describe the effects that injuries have on a range of behaviours exhibited by wild chimpanzees of the Sonso community, Budongo Forest Reserve, Uganda. Data were collected on both injured and non-injured chimpanzees in order to make a detailed comparison of the two. As previously mentioned, adult females were the age/sex class most affected by injuries in this community and in order to reduce some of the natural variation in the data only adult females with dependants were included as the focal subjects in this study.

This chapter will describe the field site, the study community and the methods used to collect the data.

#### **3.1 Introduction to the Study Site – Budongo Forest Reserve**

Budongo Forest Reserve is situated in the western section of Uganda, in the Masindi district (see Figure 3.1). The reserve has been described in more detail in Chapter One (section 1.4.1) and, as stated previously, 428km<sup>2</sup> of the 793km<sup>2</sup> reserve is forested.

##### **3.1.1 Forest structure**

The forest is described by Eggeling (1947) as lowland rainforest, consisting of three chief forest types: colonising forest, mixed forest and ironwood forest, and one minor forest type: swamp forest. They are described in detail in Eggeling (1947), and summarized here:

##### **Colonising forest**

Colonising forest, the youngest forest type, occurs along the forest edges.

Colonising forest has two stories, a low height-growth of trees, a lack of trees with





### **Mixed forest**

Mixed forest covers most of Budongo and it is the mid-way stage in the development of ironwood forest (the oldest forest type) from colonising forests. It is the most diverse forest type with many different species present (almost 50 species are recognised). It has four layers: a fairly dense bottom storey of small trees up to about 11m high, a regular second storey of trees about 11-21m high (these two storeys together form a closed lower canopy), a third storey about 21-36m, and an emergent storey of 36m and higher. This forest type contains most of the valuable timber trees in the forest.

### **Ironwood forest**

This is the oldest forest type in Budongo, and represents the climax vegetation. Seventy-five percent of the canopy, and twenty to thirty-five percent of all trees present, are of the single species *Cynometra alexandri*. There is a poorly developed understorey with the most dominant species being *Lasiodiscus mildbraedii* and *Lepidoturus lariflorus*. *C.alexandri* is said to be a superior competitor for light and nutrients in certain climatic regimes and this may be why it dominates the climax forest (Eggeling 1947).

### **Swamp forest**

This is the least common forest type, described as a type of high forest that is flooded during the wet season and waterlogged at other times in the year. In Budongo it covers thin strips of low-lying land in the bottom of valleys. It is two storeyed with an irregular canopy. Noticeable features include the presence of rattan (*Calamus*), and the abundance of lianas, strangling figs and many species of trees that are found only in swamps, including an unusual frequency of trees with armed stems or spines.

Since Eggeling's description in 1947, the forest has been altered by logging practices, including the use of arboricide treatment (see below), and natural succession. The four forest types remain but their relative proportions have



altered. Most noticeable has been the marked increase in the spread of mixed forest, at the expense of the ironwood forest, in the 40 years between 1951 and 1990 (Plumptre 1996). In a study on the effect of selective logging on primate populations in Budongo, the density of chimpanzee nests was found to have no correlation with any particular forest type (Plumptre & Reynolds 1994).

### 3.1.2 Logging history

In 1932 Budongo was gazetted as Undemarcated Forest, reserved to the Crown (Eggeling 1947). The first sawmill was established in Budongo somewhere between 1911 and 1926, but at this stage only small amounts of timber were being extracted from the forest. After 1926 the amount of timber extracted from the forest increased dramatically, the concession holders being responsible for considerable exploitation. The first of several 10 year working plans was drawn up in 1933 by the Uganda Forest Department in order to harvest timber at a sustainable level (Plumptre 1996). The most valuable timber species (mahoganies and others) are found in the mixed forest, so this forest type was targeted. The slower growing *Cynometra* species were targeted as 'weed' species and treated with arboricide in the 1950s and 1960s. This allowed openings in the canopy that encouraged the growth of mixed forest. This management practice has indeed led to an increase in the area of mixed forest at the expense of *Cynometra* forest (as stated above); a reduction of 41km<sup>2</sup> of *Cynometra* forest and 62.2km<sup>2</sup> of *Cynometra*-mixed forest, with a corresponding increase of mixed forest of 175.8km<sup>2</sup> from 1951 to 1990 (Plumptre 1996). One compartment, consisting mostly of *Cynometra* forest, was set aside as a Nature Reserve and remains untouched by logging. Currently very little mechanised logging occurs in Budongo; most trees are felled by means of both legal and illegal pit sawing, and only two legal sawmills are in operation (Plumptre et al. 2001). The Forestry Department regulates pit sawing by selling licences but, owing to a lack of men and resources to patrol the reserve, illegal pit sawing occurs.

### 3.1.3 Fauna

#### Primates

Budongo Forest is home to a variety of species of primates. Diurnal species include chimpanzees, olive baboons (*Papio anubis*), black and white colobus monkeys (*Colobus guereza*), red-tail monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*). The only nocturnal primate species that is known to occur in Budongo is the potto (*Perodicticus potto*).

#### Other fauna

Other large mammals living in the Budongo Forest include the bush pig *Potamochoerus larvatus*, duikers *Cephalophus spp.* and *Philantomba monticola*, bushbuck *Tragelaphus scriptus* and buffalo *Syncerus caffer*. In the northern part of the forest there are lions *Panthera leo* and possibly leopards *Panthera pardus*. No evidence of either was found in the study area, although calls of a lion have been heard from the Budongo Forest Project in 1992, during an extreme dry season (A. Plumptre, pers. comm). A leopard has been sighted in the far north of Budongo Forest - far north of Kaniyo Pabidi (J. Donne, pers.comm). Elephants (*Loxodonta africana* x *L. cyclotis*) were once numerous in the forest, but are now locally extinct owing to extensive poaching during the civil war. Many other smaller mammals are present including genets *Genetta genatta*, civets *Civettictis civetta*, tree hyraxes *Dendrohyrax arboreus*, and numerous species of squirrel and rodents.

Numerous bird species are present in the study area, including the crowned hawk eagle *Stephanoaetus coronatus*, a known predator of primates. The forest is home to some of the most poisonous snakes in the world including the Jameson's mamba, Gaboon viper, puff adder and rhinoceros viper. Also present are pythons, as well as many species of lizards, skinks and geckos. Invertebrate life is rich, with brightly coloured butterflies, and any number of extraordinary beetles and bugs of all descriptions. Safari ants are very common in the forest, as well as other biting insects such as flies and mosquitos.



### **3.1.4 Rainfall and Temperature**

Rainfall is plentiful throughout most of the year, with the exception of the dry season from December until March. In some years December is dry and March wet, while in others the opposite occurs (Newton-Fisher 1997). In the dry season many trees drop their leaves causing an opening up of the forest canopy. The forest is noticeably drier during this period. There is a second short season of drier conditions during the middle of the year that lasts about 4 weeks in duration, varying year to year in its timing (usually around August) and even in its occurrence.

Temperature varies with the wet and the dry season. Hotter temperatures are recorded in the dry season and cooler temperatures in the wet season. Over a period of three years (records from the Budongo Forest Project), the lowest minimum daily temperatures occurred in January - February and in July - September (Newton-Fisher 1997). The difference between maximum and minimum temperatures was greatest between December and March (Newton-Fisher 1997).

## **3.2 The Budongo Forest Project**

Vernon and Frankie Reynolds conducted the first research on chimpanzees in the Budongo Forest in 1962 (Reynolds 1963). This research was followed by other early studies conducted by Sugiyama, Suzuki and Albrecht (Albrecht 1976; Sugiyama 1968; Suzuki 1971, 1979). All these earlier studies were completed in an area near Busingiro, towards the south west of the forest. It was not until 28 years later in 1990, when Professor Reynolds returned to Uganda, that the Budongo Forest Project was initiated, at a new site near the Sonso River in the central part of the Budongo Forest. The Budongo Forest Project was set up to encompass both modern forestry and the conservation of chimpanzees. The Jane Goodall Institute initially funded chimpanzee research, and then in 1991 the National Geographic Society took over funding. One of the main aims initially was to habituate the community of chimpanzees living close to the campsite; this



began in 1991. By July 1995 all members of the Sonso community were identified and named (Reynolds 1997/8). The British Overseas Development Administration funded forestry research and general running of the camp; this funding was taken over by NORAD in 1997.

The research aims of the Budongo Forest Project are based around the understanding of the impact of human activity (both logging and the use of forest products) on the forest. The project aims to develop management strategies that allow for both conservation and human use of the forest. The main fauna species under study at the Budongo Forest Project are chimpanzees, although many other species of both flora and fauna are also studied.

### **3.2.1 Previous biological research by the Budongo Forest Project**

Research into many aspects of chimpanzee behaviour and ecology has been conducted at the project since its inception. Various topics have been studied including the demography of the Sonso community (Reynolds 1997/8), the conservation of chimpanzees in the Budongo Forest Reserve (Reynolds 1990), conservation methods such as censusing chimpanzees in Budongo (Plumptre et al. 2001; Plumptre & Reynolds 1996), diet of the Sonso chimpanzees (Newton-Fisher 1999a), nesting behaviour (Brownlow et al. 2001; Plumptre & Reynolds 1997) and infant development (Assersohm 1999). Studies of chimpanzee behaviour have focused on both male (Arnold 2001; Newton-Fisher 1997) and female (Fawcett 2000) behaviour. As well as longer term studies, there are numerous reports of anecdotal behaviours relating to chimpanzees including infant cannibalism (Newton-Fisher 1999b), lethal intra-community attack (Fawcett & Muhumuza 2000), termite eating and food sharing (Newton-Fisher 1999c), and leaf sponge drinking (Quiatt & Kiwede 1994). Research relating to snare injuries in chimpanzees has already been discussed in Chapter One (section 1.6).

Other species of primates have been the focus of research projects. Aspects of behaviour of both the blue monkeys and olive baboons have been studied (Fairgrieve 1995; Paterson 1997). Birds and invertebrates have also been the focus of some studies. The Nahan's Francolin, an endangered bird species, has been

studied (Dranzoa et al. 1997), as well as the effects of disturbed forests on birds (Dale et al. 2000; Owiunji & Plumptre 1998). Dragon-flies, butterflies and canopy-dwelling beetles have all been the focus of studies at the Budongo Forest Project (Wagner 2000, for example).

Research on ecology and forestry issues includes early studies on the ecology of Budongo (Eggeling 1947), and more recent studies focusing on information that is essential to sustainable forestry (Babweteera et al. 2000; Plumptre 1996; Plumptre & Reynolds 1994; Reynolds 1993).

Knowledge about the people that live near the forest is also an important aspect of research at the Budongo Forest Project. Studies have focused on the local farmers perspective on crop raiding (Hill 2000), hunting and the use of forest products by local people (Johnson 1996), and attitudes of local communities to forest management in Budongo (Obua et al. 1998).

The variety of research projects is essential in understanding the complexities of both the forest, and the interaction between the local communities and the forest. Without this kind of understanding conservation of the rainforest - and the endangered species within it - would be impossible.

### **3.2.2 The Sonso community**

All research on chimpanzees at the Budongo Forest Project has focused on the Sonso community of chimpanzees that live in the southern central part of the Budongo Forest. This community ranges over five forest compartments (N1, N2, N3, N4 and N15), which cover all four forest types, and both logged and unlogged forest. The community totalled 49 individuals during the current study period, with no demographic changes occurring. The following tables (3.1 to 3.3) give both the demographic distribution of the Sonso community as well as individual information including level of injury. Kin relationships stated in these tables are from behavioural observations only, as exact genetic information is unavailable at present.

## Community members

**Table 3.1** Demographic distribution of the Sonso community

	<i>Male</i>	<i>Female</i>
Adult	10	15
Sub-adult	3	2
Juvenile	6	5
Infant	1	7
Total	20	29

**Table 3.2** Male adult and sub-adult (adolescent) community members

<i>Name</i>	<i>Code</i>	<i>Age</i>	<i>Injury</i>	<i>Comment</i>
Duane	DN	Adult		Alpha
Maani	MA	Adult		
Black	BK	Adult		
Jambo	JM	Adult		
Muga	MU	Adult	Right hand missing	Son of Nambi
Bwoya	BY	Adult		
Tinka	TK	Adult	Two injured hands	
Nkojo	NJ	Adult		
Zefa	ZF	Adult		Son of Banura
Andy	AY	Adult	Recovered from snare on right ankle	Son of Nambi
Nick	NK	Sub-adult	Recovered from snare on right ankle	Son of Ruhara
Bwoba	BB	Sub-adult	Recovered from snare on left wrist	Son of Zana
Gershom	GS	Sub-adult	Recovered from snare on left wrist Fingers snared during study 2/3/00	Orphan



**Table 3.3** Female adult and sub-adult (adolescent) community members

<i>Name</i>	<i>Code</i>	<i>Age</i>	<i>Injury (other)</i>	<i>Dependants</i>	<i>Age of dependants</i>
Nambi	NB	Adult	(alpha female)	Musa (MS) Nora (NR)	Juvenile 2 Juvenile 1
Banura	BN	Adult	Congenital deformity left foot	Shida (SH)* Betty (BT)	Juvenile 2 Infant 2
Zimba	ZM	Adult	(mother of Kewayaya)	Gonza (GZ) Zig (ZG)	Juvenile 2 Infant 2
Ruda	RD	Adult		Bob (BO) Rachel (RC)	Juvenile 2 Infant 2
Ruhara	RH	Adult		Rose (RS)	Infant 2
Zana	ZA	Adult	Two injured hands	Zalu (ZL)	Juvenile 1
Kigere	KG	Adult	Missing right foot	Keti (KE)	Infant 1
Kutu	KU	Adult		Kato (KT) Kana (KN)	Juvenile 2 Infant 1
Kalema	KL	Adult	Right hand injured	Bahati (BH)	Juvenile 1
Kwera	KW	Adult		Kwezi (KZ)	Juvenile 1
Kewayaya	KY	Adult	Right hand injured	Katia (KA)	Infant 1
Janie	JN	Adult		Janet (JT)	Infant 1
Harriet	HT	Adult		Hawa (HW)	Juvenile 1
Mukwano	MK	Adult	Snare on right foot		
Sara	SR	Adult			
Clea	CL	Sub-adult			
Muhara	MH	Sub-adult			
Emma	EM	Juvenile 2	(Orphan)		

\*Shida, Banura's juvenile daughter, has two snare injuries. She is missing the whole of her left hand and has a cord snare on her right foot (see Figure 2.7). No other juvenile or infants are injured.

The kin relationships given in Table 3.2 are based on general association patterns and behaviour seen among individuals. The kin relationships of infants and juveniles, given in Table 3.3, are based in most cases on birth, but for some cases are also based on association with the mother.

### Age / sex categories

Table 3.4 shows demographic categories used in this study, they are taken from those used at the Budongo Forest Project (latest version March 1998).

**Table 3.4** Demographic categories used at the Budongo Forest Project

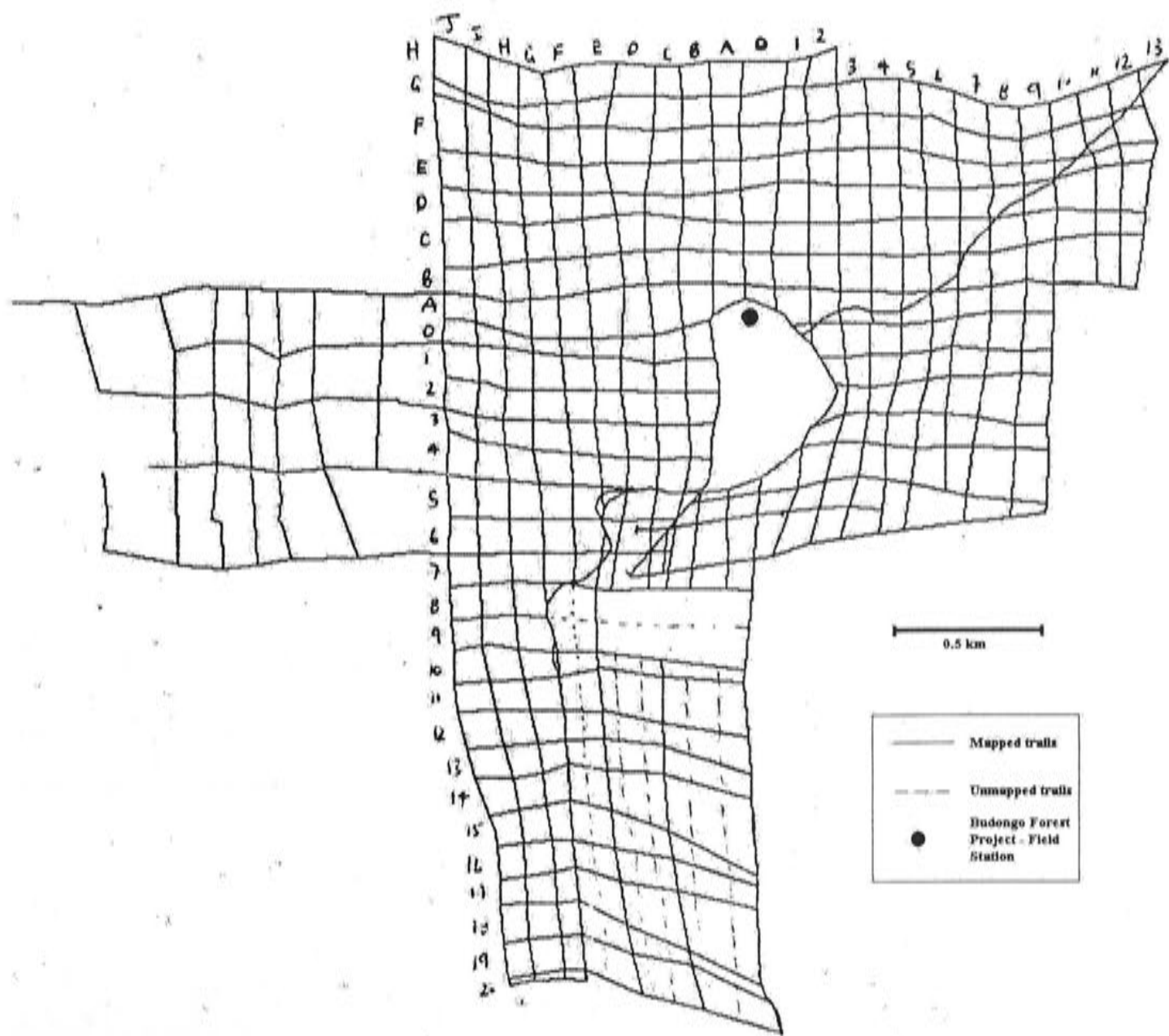
<i>Category</i>	<i>Definition</i>
Infant 1	0-2 years: moving with mother, not yet weaned from mother's milk
Infant 2	2-4 years: moving away from the mother, feeding on foods other than mother's milk but not yet fully weaned. Still carried by the mother. Infancy terminated by the birth of the next sibling.
Juvenile 1	4-6 years: still close association between mother and offspring, but the juvenile is now feeding and moving, on the ground and between trees, independently.
Juvenile 2	6-8 years: increasing independence from the mother. May or may not always be in the same sub-group as the mother. When feeding in the same sub-group is often far from the mother.
Sub-adult male	8-12 years: development of testes. Beginning to challenge females for dominance.
Sub-adult female	8-10 years: beginning of full sexual swellings, may be irregular. Adult males not very interested when in oestrous. No offspring.
Adult male	Testicular development complete. Face fully black. Now dominates all females and challenges other males for position in hierarchy.
Adult female	Has offspring, has regular swelling cycles.
Old male and female	Baldness developing around the head and lower back

The system of ages shown in Table 3.4 is a rough guide; there is a large amount of inter-individual variation.

3.2.3 The trail system

The trail system surrounds the field station and covers a large proportion of the Sonso chimpanzee community's home range. Originally two kilometre trails were cut in the forest for a census project (Plumptre & Reynolds 1994), these trails are now the basis of a much more detailed trail system in the compartments surrounding the campsite (see Figure 3.2). Trails have been cut in north-south and east-west directions, and they intersect to give 'blocks' of generally 100m by 100m. Thick vegetation, fallen trees and difficult topography mean that the accuracy of these blocks sometimes wavers. The blocks are each numbered and a small tag is located at each corner so as to assist researchers to keep track of their

Figure 3.2 Trail system in the Sonso region of the Budongo Forest





position in the forest. Trail cutters employed by the Budongo Forest Project keep all the trails as clear as possible. Humans, chimpanzees and other forest animals use these trails for ease of locomotion through the dense areas of forest. Well-used animal tracks are also present in the forest, and are used in conjunction with the existing man made trail system.

### **3.3 Aspects of this study**

#### **3.3.1 Study period**

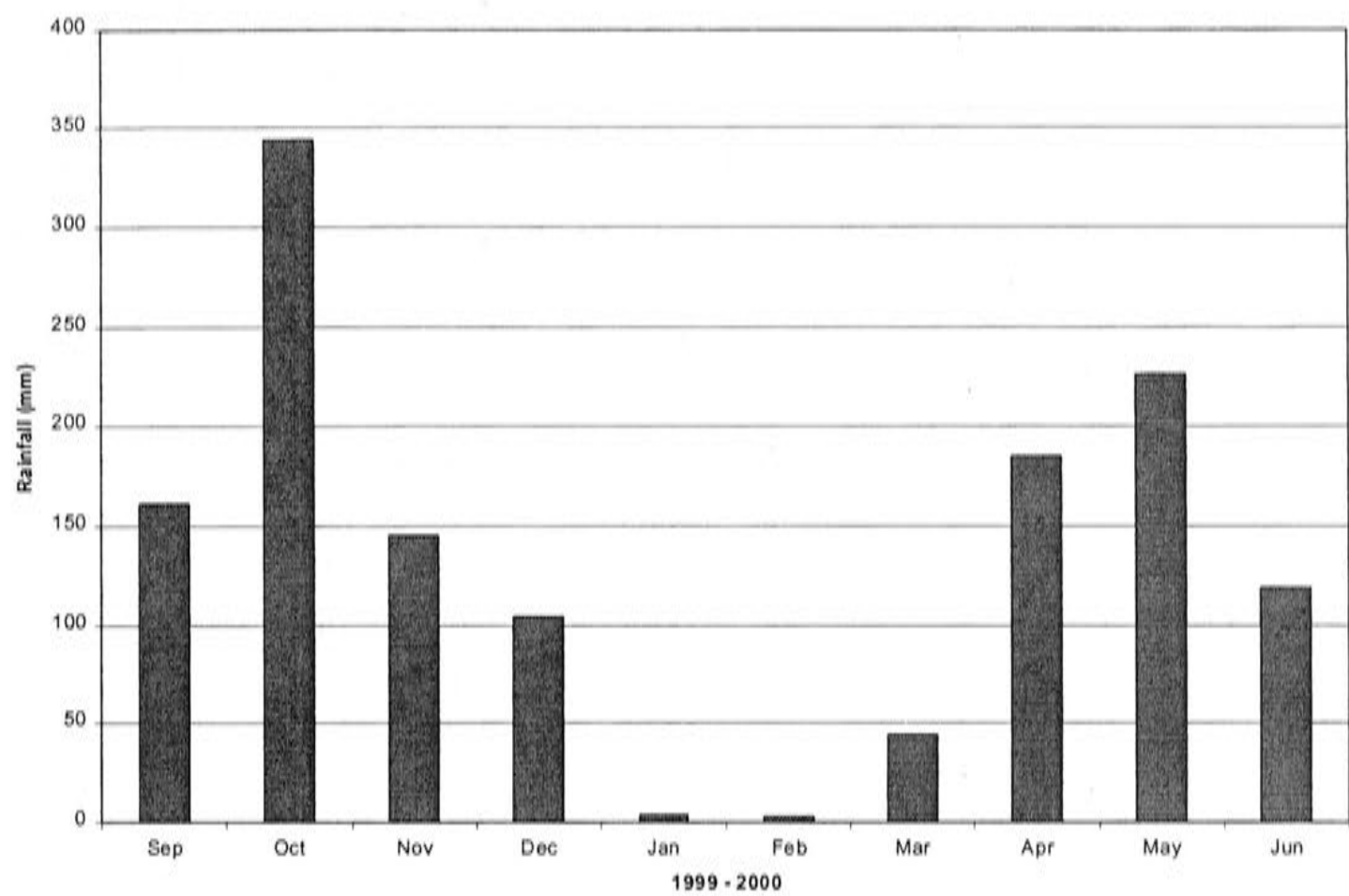
I arrived at the Budongo Forest Project on the 16<sup>th</sup> October 1999. I spent the first month learning to identify the chimpanzees and testing research methods. The first 'real' data were collected on 17<sup>th</sup> November 1999. Data were collected until 18<sup>th</sup> December 1999 when the project closed for the Christmas period. The project reopened on 4<sup>th</sup> January 2000 and data were collected again from the 5<sup>th</sup> January 2000 until the end of the study period on the 15<sup>th</sup> of June 2000.

#### **3.3.2 Rainfall and temperature during study period**

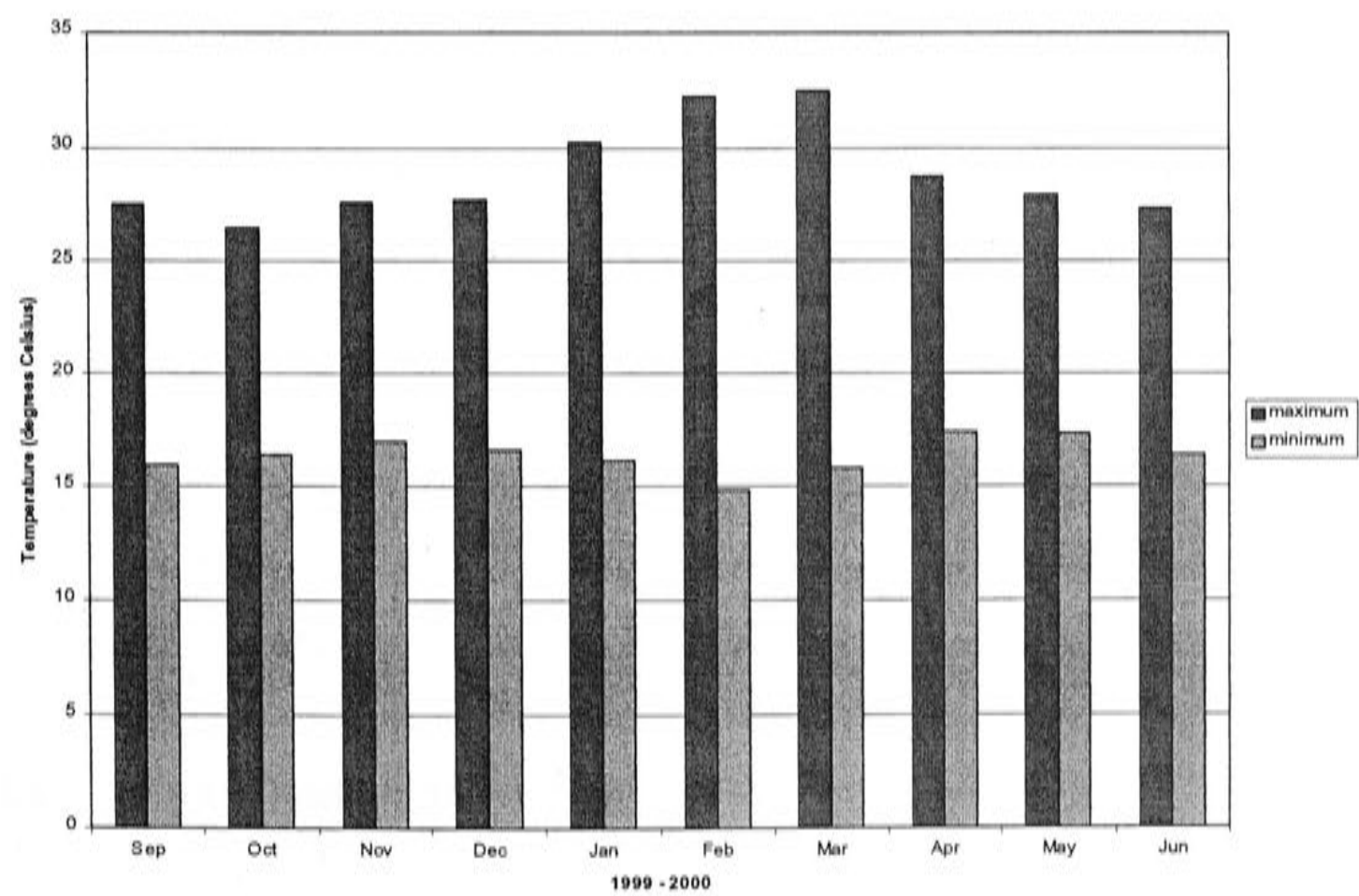
Figure 3.3 shows the monthly variation in total rainfall recorded for the study period - September to June. The dry season began in January and continued until the end of March; all other months are considered as part of the wet season. A second short dry period was not recorded as the study period did not coincide with its timing.

The temperatures for the period of the present study are plotted in Figure 3.4. The lowest recorded temperature was 10°C and the highest recorded temperature was 35°C. The mean temperature was highest during the dry season (Jan – Mar) and lower during the wet season (Sep – Dec, Apr – Jun). The difference between maximum and minimum temperatures was greatest in February and March.

**Figure 3.3** Monthly variation in total rainfall at Budongo Forest Project: September 1999 – June 2000.



**Figure 3.4** Monthly variation in mean maximum and minimum temperatures – September 1999 – June 2000.





### **3.3.3 Sampled individuals**

This study focuses on the adult females with dependants of the Sonso community. Out of the 15 adult females listed above (Table 3.3), 12 were the focal subjects for this study, and five of those had injuries. Mukwano and Sara were not focal subjects, as neither had dependant offspring, and in addition Sara spent large amounts of time away from the community. Harriet was not included as a focal subject as she seemed to be present in the community only when in oestrus and insufficient data were collected on her.

For some analysis extent of injury has been included. Zana, with injuries to both hands, and Kigere, who is missing a whole foot, are seen as having the most severe injuries. Kewayana and Kalema have only one hand injured, and Banura has a swollen foot: these three are seen as having less severe injuries. The fact that Zana and Kigere both showed difficulties in balancing, both when moving and feeding, were also factors that led to their being included in the category of most severe injuries.

### **3.3.4 Field assistant**

During my study at Budongo I was accompanied by my field assistant, Karamagi Joseph, who helped with the location and identifying of chimpanzees. As the vegetation in parts was often very thick it was necessary to have Joseph's assistance in determining the movements of the chimpanzees, especially those joining and leaving groups. Joseph would focus on this while I was collecting data on the focal subject. Often we managed to relocate chimpanzees after they disappeared into thick vegetation by going in separate directions. We were able to communicate by a series of whistles in order to find each other and the chimpanzees again.

## **3.4 Data collection methods**

Chimpanzees were found each day by a number of methods. On most occasions chimpanzee calls could be heard from camp early in the morning and so they were



found by following the direction of the calls. Visiting the place that chimpanzees were last seen on the evening before, or visiting known fruiting trees, were also methods of locating chimpanzees. Sometimes chimpanzees were found randomly by unexpectedly seeing them on one of the trails. The method of location was recorded for each observation period: 50% of chimpanzees were found by visiting a known food tree, 42% were found by hearing morning calls, and 8% were found by random methods.

Chimpanzees were observed for 30-minute observation periods, using both focal animal sampling and scan sampling. Observation periods were rotated amongst focal subjects (see below).

### **3.4.1 Focal animal sampling**

Individual chimpanzees were observed using the focal animal sampling technique described by Altmann (1974). Data were recorded by hand on prepared data sheets using a series of behavioural categories (see Table 3.5). Focal animal sampling was chosen in order to gain detailed data on times spent in certain behaviours. 30 minutes was chosen for the observation period as it was difficult to stay with some of the females for a longer period owing to lack of habituation, and also to the thickness of the vegetation in some parts of the forest. All day follows were considered at the onset of the study, but they had been attempted in previous studies and were found to be unsuccessful, as some of the female subjects were not fully habituated (C. Assersohm, pers. comm). All day follows were attempted but it was quickly established that, for at least some of the adult females, it was indeed impossible to complete a full day follow.

Sampling rules were made in order to determine the order in which subjects were observed (see section 3.4.3). The sampling rules and the rotation of focal subjects aimed to enable observations to be spread equally between all individuals over the study period.

In order to reduce dependence in the data, no individual was observed more frequently than once every 90 minutes, that is a full hour was allowed to pass

before the end of one observation period and the beginning of the next. This method is derived from one used by Wrangham and colleagues (Wrangham et al. 1996). A minimum 5-minute break was taken between each observation period in order to reduce observer fatigue and to further reduce dependence in the data.

### **3.4.2 Scan sampling**

Scan sampling (Altmann 1974) was used to measure group composition and proximity of individuals to the focal chimpanzee. Records of all individuals present in a group, or believed to be present (i.e. had been seen to enter or travel with the group and had not been seen or heard leaving, usually confirmed at a later stage when the group began travelling or individuals came into sight) were taken every 15 minutes, during the 30-minute observation period, for the focal subject. 'Group' was defined as all individuals within 50m (see section 4.4.2 for more details).

The individuals within one metre and five metres of the focal were recorded on each scan. It is possible to assume that individuals that are in close proximity to each other bond more closely with each other, and so that data collected on the proximity and association of individuals can be used to determine association partners within a community (Hayaki 1988; Kawanaka 1993). The measure of proximity also gives some insight into the tolerance of different individuals to each other. It has previously been argued that the distance between two individuals provides a rough measure of mutual tolerance and respect (Quiatt et al. 1994). Those individuals found to be within one metre of each other, i.e. within arm's reach, are measured as the closest proximity and thus represent a high level of tolerance. The five-metre proximity was included to gain data on a different level of association. Five metres was chosen, as distances greater than five metres may not be informative about the tolerance of the focal chimpanzee to that individual, considering the variable and complex organization of locomotion substrates in three dimensional space (D. Quiatt, pers. comm.). For example, an individual may be 10 metres away from another individual in two dimensional space, but if one takes into consideration the three dimensional space, the individuals may be on completely different branches of the same tree, and may

have to return to the trunk of the tree before reaching each other, perhaps covering a total of 15 metres or more. Also measurements beyond five metres would increase the flight distance and thus greatly reduce the level of tolerance required. Thus, the larger the measure of proximity, the less likely that it may be saying something 'real' about tolerance between individuals. Five metres was also a useful measurement as it was generally easy to identify other individuals in this range of the focal.

On each 15-minute scan, group activity, weather, location and grooming activities were also recorded.

Five-minute scan samples were also taken. During each 30-minute observation period, seven five-minute scans were taken focusing on the behaviour of the youngest offspring. All adult females had an offspring between the age categories of Infant 1 and Juvenile 1, and no females had two offspring within these age categories, although some had a second dependant of the age class Juvenile 2. Scan samples are too difficult for the age class Juvenile 2, as by definition they can be found travelling in a separate group from the mother. Five minute scans were chosen as it seemed frequent enough to collect useful data, but not too frequent that it takes time out of the focal sample on the mother.

The position of the mother in the tree was also recorded at each five-minute scan. A simple, relative measure was used to determine whether injured mothers tend to use branches closer to the main trunk rather than going out to the extremities. Each tree over approximately 40cm d.b.h. was divided visually into three parts. The radius, from the main trunk out to the far extremities of the branches was divided into: (1) the third closest to the main trunk, (2) the third farthest from the main trunk and (3) the third in between.

### **3.4.3 Sampling rules**

- When chimpanzees were located, if only one mother and her dependants were present, then the mother was the focal subject. After the completion



of one 30 minute observation period a new search was conducted for other mothers. If no other individuals could be found, then further samples of the first mother could be taken, ensuring that a full hour had passed since the end of the previous period. If more than one mother and dependant were located, a sampling priority was used to determine the focal subject, and the following order of observation periods.

- Sampling priority: a continuous tally was kept for the number of observation periods completed on each individual. A list of individuals was created with the least sampled individuals at the top. The order in which individuals present in the group were sampled depended on the order of the list.
- A continuous tally was also kept in which time of day of samples for each individual was recorded. Sampling from all times of the day was also considered when choosing focal subjects, although this was secondary to getting approximately equal numbers of observation periods on individuals.
- During the early parts of the study, under-sampled individuals were observed during the one-hour break between observation periods. This was done just in case the amount of data collected at the end of the study period was lacking for these individuals. As this was not the case, none of these observation periods were used in any of the analyses.

#### **3.4.4 Behaviour codes**

Both state and event data (Paterson 1992) were collected throughout the study period. Table 3.5 shows the behavioural categories used for state behaviours. Event data are not described here, and were not used in the analysis because of the small amounts collected. It was often difficult to gain accurate event data because of visibility, and in general adult females were involved in far fewer interactions than other age/sex classes. Despite this, event data involving dominance are briefly mentioned in Appendix 2.

**Table 3.5**      Behavioural states

<i>Code</i>	<i>Description of behaviour</i>
Out of sight	The focal individual is not visible
Resting	The focal is lying still with eyes open or closed
Grooming	Focal is grooming another individual, defined as parting hair in an attempt to pick at the skin
Being Groomed	Focal is being groomed by another
Mutual Grooming	Two individuals (one is the focal) are grooming each other at the same time
Group Grooming	Focal is involved in grooming behaviours with more than one other individual at the same time
Self Groom	Focal is grooming self
Play Tickle	Focal is playing with another in a relaxed manner
Play Chase	Focal is playing with another by chasing
Play Rough	Focal is playing vigorously; wrestling, tumbling,
Play Alone	Solitary play
Feeding	Includes manipulating food item, ingesting, wadging, paying attention to another feeding, searching for food (feeding was not the focus of this study so all behaviours were combined)
Move on ground	Individual moving on ground by itself
Move on ground with infant	Individual moving on ground and carrying dependant
Move in tree	Any arboreal movement
Move in tree with infant	Any arboreal movement carrying dependant
Building Nest	Using vegetation to create a nest
Nested	Out of sight in nest, or obviously sleeping/resting in nest

Behavioural states were also recorded for infant behaviour. These are described in the relevant chapters. Data collected during the 15 minute and five-minute scan samples are also explained in the relevant chapters.

Anogenital swelling phases were given numerical codes: 0 = no swelling; 4 = full swelling; and 1, 2, and 3 were stages in between. When females were in the partial swelling stages of 1 and 2 they gained little sexual attention from adult males. When in the partial swelling stage of 3 and the full swelling stage of 4, females gained considerable sexual attention from males.

#### **3.4.5 Number of observation periods**

As well as referring to the sampling rules (above), care was also taken to make sure that subjects were observed evenly in both seasons and at different times of day. Tables 3.6 and 3.7 show the number of total observation periods on each individual, and the numbers of observation periods in each season and at different times of the day.

Table 3.7 shows that all individuals are represented in both seasons but some individuals are under-represented (e.g. Zana and Ruhara in the dry season). Some individuals proved difficult to find at certain times, perhaps because they were travelling alone, or ranging in areas off the marked trail system. Many more observation periods were collected on all individuals in the morning than in the afternoon. Early afternoon hours were the most difficult time to observe the chimpanzees, as often they would rest on the ground in thick undergrowth, where the visibility was poor. Even if it were possible to remain with the chimpanzees during these hours, it was very difficult to collect data as doing so involved moving around on the ground to gain visibility, and that usually meant disturbing an otherwise restful group of chimpanzees. If chimpanzees were lost over the middle part of the day, they were often found again in the late afternoon, as the temperature dropped, and they began travelling, feeding, and more importantly, calling again.



**Table 3.6** Number of observation periods and total time each individual was observed. Also included is the number of observation periods recorded outside the one-hour rule (see section 3.4.3).

<i>Focal</i>	<i>Injury status</i>	<i>Number of observation periods</i>	<i>Total time observed (minutes)</i>	<i>Extra observation periods (not used in analysis)</i>
Banura	Congenital deformity	33	990	5
Janie		38	1140	1
Kigere	Injured	36	1080	7
Kalema	Injured	41	1230	0
Kutu		31	930	1
Kwera		45	1350	2
Kewayaya	Injured	44	1320	4
Nambi		38	1140	1
Ruda		34	1020	3
Ruhara		29	870	4
Zana	Injured	39	1170	18
Zimba		43	1290	1
Total		451	13530	47

### 3.4.6 Season

Data were collected in both the wet and the dry season. It was appropriate in the data analysis to determine the effect different seasons had on the results, and so season was used as a factor in much of the statistical analysis (see section 3.5). It must be noted that data were not collected for a full 12-month period. Data were collected for three months in the dry season and five months in the wet season: a total of 219 observation periods were collected in the dry season, and 232 in the wet season (Table 3.7). A previous study found considerable variation between

**Table 3.7**      Number of observation periods in each season and at different times of day

<i>Focal</i>	<i>Season</i>		<i>Hour of day in which observation period started</i>										
	Wet	Dry	7 am	8 am	9 am	10 am	11 am	12 am	1 pm	2 pm	3 pm	4 pm	5 pm
BN	13	20	8	8	5	2	2	1	2	1	1	2	1
JN	17	21	7	9	7	6	2	2	1	1	1	1	1
KG	19	17	8	8	3	2	2	5	2	0	1	2	3
KL	18	23	10	9	4	5	3	2	0	0	3	4	1
KU	18	13	7	10	3	4	1	1	0	0	1	1	3
KW	18	27	10	6	6	8	3	4	1	0	2	3	2
KY	17	27	7	7	5	7	7	1	1	1	2	4	2
NB	17	21	7	10	5	6	2	3	1	0	2	0	2
RD	18	16	5	8	3	2	3	3	2	1	1	4	2
RH	22	7	5	6	5	3	1	2	1	1	0	1	4
ZA	33	6	7	5	8	5	1	3	4	2	1	1	2
ZM	22	21	3	9	9	6	3	0	2	1	2	6	2
Total	232	219	84	95	63	56	30	27	17	8	17	29	25

NB. The 7am time includes any samples that began earlier, and the 5pm time includes any samples that began later than these times.

the foods available and used by the chimpanzees of the Sonso community in the wet and the dry season (Stokes 1999). In the current study, food seemed to be scarcer in the dry season (personal observation), and chimpanzees appeared to range more widely to find food. This was not the case in an earlier study from Budongo where there was no period of food shortage in the dry season, though it was suggested that the patterns of food availability could change from year to year (Newton-Fisher 1999a). The possible changes in food availability may affect the behaviour of chimpanzees during each season, and so differences between the wet and the dry season were analysed, despite only having 8 months of data available.

### 3.5 Data analysis methods

Data were transferred from data sheets to the computer program SPSS for Windows, 7.0. This was a lengthy process, but extra time was allocated for re-checking in order to eliminate any errors in the data.

Data were then grouped into behaviours or categories and total time spent or total number of occurrences for each were calculated. Percentages were calculated and graphs were drawn in order to try and examine the general trends in the data. Where it appeared that differences between injured and non-injured individuals might be occurring, then statistical analysis was completed.

Each data set was analysed in separate ways according to the nature of the data and the questions that were asked. Linear models were used to analyse most of the data (for exceptions see below). Focal animal sampling resulted in continuous data (measuring data, or data on a time scale), whereas scan sampling resulted in discrete data (count data). A different type of linear model was used for each different type of data (Davidian & Giltinan 1995; McCullagh & Nelder 1989).

Linear models were chosen as the method of analysis as they allow for the testing of the effects of multiple explanatory variables on the response variable. This is important owing to the difficulties inherent in analysing data collected on chimpanzee behaviour. This thesis addresses how injury affects a specific behaviour, for example time spent moving. There are many variables that may also be affecting the time a chimpanzee spends moving, for instance the time of day of the observation period. Linear models allow these variables to be included in the analysis. These variables can be either factors or covariates. In this study variables are factors such as injury status, age of dependant, number of dependants, season of observation and time of day of observation.

In some cases graphs were drawn to explain the results found in the model. A measure of error was used in each figure expressing the statistical analysis. Where error bars are used they refer to 95% confidence intervals, which are used to show



the variation in the means. Where the least significant difference (lsd) is used it refers to the minimum distance needed to have a significant difference. This shows the difference between means. The logit of the measure being analysed was used in some of the figures, as proportions need to be transformed to the logit scale in order to normalise the data.

### **3.5.1 Focal animal sampling**

Continuous data collected during focal animal sampling were analysed using mixed linear models. All data were analysed as a proportion (e.g. time chimpanzee spent moving / total time chimpanzee observed). Proportions are not usually normally distributed, so the proportions were transformed to the logit scale to normalise the data.

$$\text{logit}(p) = \log(p / 1-p) \quad \text{where } p = \text{proportion}$$

Mixed linear models are parametric models that assume several levels of variation in the data. Mixed linear models are very similar to simple linear models, but include multiple levels of variation. Mixed linear models were used in the analysis of the focal animal sampling data, as there is more than one level of variation in the data. This can be seen when looking at the nature of the continuous data from the focal animal sampling:

- observation periods on 12 focal subjects
- multiple observation periods (~30) on each focal subject (rather than single measurements made on many focal subjects)
- multiple factors possibly affecting the response (such as injury status, season)

Therefore variation exists between observation periods and between focal subjects. The mixed linear model takes into account the multiple measurements on each focal subject by allowing for two levels of variation – variation between focal subjects and the variation within focal subjects (or the variation between observation periods).

### 3.5.2 Scan sampling

Discrete data, collected by means of scan sampling, were analysed using a binomial Generalised Linear Model. The data are binomial in that there are always so many counts out of a total (e.g. for the 5 minute scan data for infant playing, an infant will play for, say, 2 counts out of the total of 7 possible scans in any one observation period). For Generalised Linear Models only one level of variation in the data was assumed, as it is simpler not to include multiple levels of variation, i.e. within observation periods and within focal subjects, in this context.

The main difference between linear mixed models (used for continuous data) and generalised linear models is that the linear mixed models assumes that the data are from a normal distribution, whereas the generalised linear model allows for other distributions of the data to be used – in this case a binomial distribution has been used.

In both cases the linear model is the framework in which the statistics are used. The statistics used to answer the questions asked in this thesis are the Change in Deviance Statistic (F test) or the Wald Statistic. These statistics have a chi-squared distribution, so the chi-squared table of values is used. Significance levels of  $p < 0.05$  are used throughout, unless otherwise specified. For analyses where simultaneous tests are carried out on the same data set, the Bonferroni correction method is used to change the significance level used (Howell 1997). The significance level is changed to  $\alpha / m$  where  $\alpha$  = normal significance level (0.05) and  $m$  = the number of simultaneous tests.

### 3.5.3 Exceptions

1. Proportions of time (i.e. between 0 and 1) are the measure used for continuous data analysed by linear mixed models (see above). When a particular behaviour does not occur in an observation period the proportion (for that behaviour) then equals 0. Often there were too many zero observations for the data to be well modelled by a normal or binomial distribution, and a two-stage approach to modelling was used. An example of this is the time a chimpanzee

spent grooming other community members: it happened infrequently, and so created many observation periods with a zero proportion. In a case such as this the data were firstly analysed for the presence or absence of a particular behaviour in any observation period using a binomial Generalised Linear Model (when the data are looked at in this way they become binomial in distribution). If a difference was found, then a linear mixed model was used to analyse only the observation periods where the particular behaviour occurred. For the above example, only the observation periods where chimpanzees were grooming other community members were included. Then it was possible to determine, out of the reduced observation periods, if there was a difference in the amount of time spent in that behaviour for the factors being analysed (i.e. injury, age of infant, etc.).

2. A simple test of difference in binomial proportions was also used for data that were unable to be analysed by any of the above methods, using the normal approximation to the binomial or Z-test (Jaccard & Becker 1990). This analysis was used in cases where the behaviour was rarely seen (e.g. group grooming).

3. Dyadic Association Index, Cluster Analysis and Social Time Index were used in the analysis of data on association and proximity. For more details of these methods see section 4.4.3.

N.B. All statistics were conducted with the assistance of the Graduate Statistical Consulting Unit for the Australian National University.



## Chapter Four

### **The impact of injuries on free-living chimpanzees – group size, composition, association and proximity relations**

*A large feeding group gathers early in a fruiting fig tree. As the morning progresses more chimpanzees join this group. By 9am there are 20 individuals in the tree, a mixed group with adult and sub-adult males, as well as females with their dependants and nulliparous females. Gradually as the morning wears on small groups leave the fig tree, first a rowdy group of adult and sub-adult males responding to calls far off to the west, then a nursery group of a few mothers, their dependants and sub-adult females head south. Others quietly leave alone. By 10am there are only three adult females remaining in the tree with their young. Not long after this two of the mothers leave together, and Zana remains with her juvenile son, Zalu. Zana has severe injuries to both hands. They stay alone in the tree, both feeding and resting, until much later in the afternoon, when they finally descend and disappear into the undergrowth. (Budongo Forest: December 1999)*

#### **4.1 Introduction**

Chimpanzees throughout their range live in large communities numbering anywhere from 20 - 30, to over 100 individuals (Boesch & Boesch-Achermann 2000; Nishida 1990). At Budongo only one community, the Sonso community, has been fully habituated and it numbers 49 individuals. The structure of chimpanzee society is a flexible one described as fission-fusion, that is, individuals form temporary sub-groups within the larger more stable community, and these sub-groups change in size and composition considerably on a daily basis (Goodall 1986; Nishida 1968; Sugiyama 1968). A variety of sub-groups are formed including: mothers' groups (or nursery groups); adult groups; mixed age and sex groups; bands of males (Reynolds 1963); individuals travelling on their own (Nishida 1968); parties of juveniles and sub-adults, and females without young (Sugiyama 1968). Association patterns vary between individual chimpanzees; the fission-fusion society allows for each chimpanzee to spend

different amounts of time with other individuals in the community. Two chimpanzees, not necessarily kin, that spend a lot of time in the same group, and in close proximity to each other, have been termed 'friends' (Boesch & Boesch-Achermann 2000; Goodall 1986). Choice of spending time with another individual is based on the benefits of company versus the costs of competition.

It has been questioned in previous studies whether injured chimpanzees have the same social grouping and association patterns as non-injured chimpanzees. Ghiglieri (1988) observed that chimpanzees at Kanyawara, Kibale N.P., with injuries from snares, were unable to keep up with a travelling group, which altered the social groups they formed. Researchers working with the study community in Budongo Forest have made observations of injured chimpanzees that suggest both that their association levels may be affected by their injuries (Fawcett 2000; Newton-Fisher 1999a), and unaffected (Quiatt & Reynolds 1994). There are also examples from other primate species (see Chapter 2), instances where social grouping and association is both affected and non-affected by injuries: the severely injured Japanese macaque who ignored strong family bonds and joined a higher ranking group in order to gain access to food, and mountain gorilla and gibbon groups who waited for injured members when they were unable to keep up. It is unknown then how injury affects social grouping and association in chimpanzees and other primates.

This chapter will review the types of factors that may affect social grouping and association in chimpanzees. Then following a statement of the aims, analysis will focus on how injury in female chimpanzees of the Sonso community may affect the formation of groups and choice of association partners.

## **4.2 Factors affecting group formation**

There are many factors that may affect the composition and size of each group formed, and also the association patterns seen between individual chimpanzees. In the following examples it must be noted that many different sites across Africa are discussed; not all are directly comparable to the study site. Chimpanzees living in forest habitats, such as the Budongo, Kibale and Tai communities, are directly



comparable (Boesch & Boesch-Achermann 2000); the Gombe and Mahale communities, living in woodland habitat, are not.

#### **4.2.1 Group size and composition**

##### **Food resources and competition**

The size, distribution and quality of food patches are factors that may affect the size of groups formed by chimpanzees (Goodall 1986; Itani & Suzuki 1967; Nishida 1968; White & Wrangham 1988). Generally it is hypothesised that party size is large when availability of food is great, and small when food availability is low. In Kibale forest, Uganda, this hypothesis was tested and it was found that food patches with relatively high densities of fruit did support significantly larger foraging parties (Isabirye-Basuta 1988). More recent analysis shows exceptions to this hypothesis. A study at Kalinzu Forest, Uganda, found no relationship between party size and fruit abundance and distribution (Hashimoto et al. 2001). Research from the study site, Budongo Forest, found that although party size increased as food patch size increased, there was no such relationship with habitat-wide measures of food abundance, so both the dispersal and abundance of food needed to be considered when analysing the effects on grouping (Newton-Fisher et al. 2000). A second study did find that party size was positively correlated with increasing food availability, but for all-male parties and sexual parties, and not for all-female parties (Fawcett 2000).

##### **Sex of the individual**

Grouping patterns seem to be affected by foraging strategies in different ways for each sex. Females seem to be more concerned with maximising their energy intake in order to maintain a high reproductive rate, and thus are semi-solitary, which gives more time for foraging and reduces feeding competition. Males, on the other hand, are more inclined to forego an optimal foraging strategy in order to optimise sexual opportunities, and have time to focus on other activities such as cooperating to defend the boundaries of the communities' range (White & Wrangham 1988; Wrangham & Smuts 1980). Dunbar (1988) states that group



composition can be greatly influenced by the difference in grouping strategies for males and females; females choose to group according to the best available food sources owing to the importance placed on rearing and producing offspring, while males group in a way that allows them to gain control over the largest group of breeding females.

### **Oestrous state**

Goodall (1986) described sex as playing a 'powerful' role in chimpanzee society. The fluid nature of the fission-fusion society allows males to seek out and form groups with females when they are receptive. Party size was greater when females with sexual swellings were present (Goodall 1986). A recent study from Mahale Mountains National Park found that regardless of their oestrus state all cycling adult females were found in mixed-sex groups as often as males, while non-cycling females were seen in mixed-sex parties less often than cycling females or males (Matsumoto-Oda 1999). Research involving the study community, the Sonso community, also revealed that parties containing a cycling female were significantly larger than those with no cycling females, and that parties with two cycling females were larger than parties with only one cycling female (Newton-Fisher 1999a).

### **Hunting**

The presence of oestrous females (cycling females with maximal genital swelling), therefore, strongly influences chimpanzee grouping patterns. The decision to hunt by chimpanzees at Gombe seems also to be affected by the number of oestrous females, as well as the number of adult and adolescent males in a group and the total size of the party. The larger the numbers of any of these are, the more likely it is that the group will hunt red colobus (Stanford et al. 1994). Stanford et al. (1994) argue that it is difficult to determine whether the female reproductive cycle may indirectly cause the seasonal differences found in hunting patterns, also whether the males gather around oestrous females or oestrous females join large parties that have formed for some other reason. It is also possible that male chimpanzees hunt in order to be able to give food to oestrous

females, in the hope that females prefer to mate with these males. This cannot be the only factor responsible for hunting, as males hunt when there are no females as well (Stanford et al. 1994). Hunting then seems to affect, possibly directly or indirectly, the size of groups formed by chimpanzees. Boesch (1996) also found that hunting rate did explain some variations in party size in Tai chimpanzees (Boesch 1996).

### **Predation**

Predators of chimpanzees include both leopards (Boesch 1991; Hiraiwa-Hasegawa et al. 1986) and lions (Tsukahara 1993). In forests where predators are present, it would seem that small groups that are commonly formed in a fission-fusion society, would be at a high risk of predation. The social grouping of chimpanzees at Tai is affected by the risk of predation in two ways. Firstly foraging groups are small, but are close enough to be in auditory contact with each other. Although the typical predator avoidance strategy is to form large groups, the visibility in the forest at Tai is very low which means the noise made by a large group of chimpanzees would attract predators, despite the number of extra eyes available to spot leopards. Secondly they are mostly found in groups with the best defence capabilities, that is mixed and all-male groups (Boesch 1991). While both lions and leopards have been observed in the northern part of the Budongo Forest Reserve (see section 7.7.2), they have not been observed near the study area. The affect the “potential risk” of predators (Boesch 1991; Dunbar 1988) may have on behaviour of chimpanzees in Budongo is discussed in more detail in Chapter Seven.

### **Combination of social and ecological factors**

Boesch (1996) found that in the Tai Forest most of the variation in party size was determined by general fruit availability, sexual opportunities and the hunting rate. Thus both ecological and social aspects are interacting to explain the social organisation.



Matsumoto-Oda et al. (1998) looked at the factors affecting party size in chimpanzees of the Mahale Mountains. They found that during seasons of low fruit availability, when the number of food items eaten was high, the party size was small. They also found that the number of cycling females that came into oestrus had an effect on the size of mixed parties; so larger parties coincided with large numbers of females in oestrus. They found no relationship between these two factors, suggesting that both independently have an effect on group size and structure, rather than one single factor controlling group formation (Matsumoto-Oda et al. 1998). The study also reported a relatively consistent annual cycle of the seasonal variation seen in party size.

Thus it appears that the formation of groups in chimpanzees is a complex one, not easily explained by a single variant. It is possible that the inclusion of injured chimpanzees in a community also affects the social grouping seen, especially if injured chimpanzees are unable to keep up with travelling groups or if other group members show a lack of tolerance towards them.

#### **4.2.2 Association and proximity**

Previous studies have also focused on the many factors that affect the individual-individual associations seen in wild chimpanzees. Age, sex and social rank of the individual, kinship and individual choice are all factors that are discussed in detail in this section. The factors described above that affect group size and group composition also concern association patterns between individual chimpanzees. This is because these factors affect the size of the group formed, and the size of the group restricts the choice of who to associate with.

##### **Age and social rank**

Both age and social rank are factors determining association, and because of this, association partners change over time. For example a young juvenile male will spend all his time in close association with his mother, and then as a sub-adult he will spend his time predominantly with adult males (Hayaki 1988). A young female will spend all her time in close association with her mother until she begins



to cycle and have periods of oestrus, after which she will spend more time with adult males either of her own or a neighbouring community. Some females transfer to another community and lose contact with their mother altogether (Goodall 1986). Late adolescent males, although they are still able to travel with older males, are not well tolerated by them. Prime and senior males on the other hand are able to associate with each other intimately (Kawanaka 1989). Both age and dominance rank can be seen to affect the association and proximity of chimpanzees in fairly predictable ways for each age and sex.

### **Kinship**

Family members that remain in the same community are likely to remain close associates throughout their lives. This is most evident in male maternal siblings that are born in succession (i.e. around 5 years apart). As they spend many of their younger years playing and travelling together they tend to form strong social bonds. As they grow older and begin to rise in social rank they are able to support each other in times of social conflict. With a friendship of this kind one male sibling almost never takes sides against the other (Goodall 1986).

Mothers and daughters also have very close social bonds and if the daughter does not migrate to another community the two can spend a great deal of time in association. A good example of this is two of the adult females in the study community: Zimba and Keway. Zimba is thought to be the mother of Keway, and both females have infants of about the same age. They spend a lot of time in close association, grooming, travelling and allowing their infants to play with each other (personal observation).

### **Sex of the individual**

Association patterns have been found to be different for male and female chimpanzees. Male chimpanzees form strong bonds with other males in their community, and have a higher tendency to group than other age/sex categories (Nishida 1979). Boesch and Boesch-Achermann (2000) compared the average association of individual chimpanzees of the same sex, and of different sexes,

from four different field sites. In all cases males, on average, are more strongly associated with other males, than are females with females, or males with females, although there are cases of particular female dyads having high association levels (Boesch & Boesch-Achermann 2000).

A recent study at Ngogo, Kibale N.P., proposed an exception to the commonly agreed association patterns (Pepper et al. 1999), such as the ones compared in Boesch and Boesch-Achermann's (2000) study. The methods generally used in such studies of association do not allow for the differences that are seen in general gregariousness between males and females; with males being more gregarious than females (Halperin 1979; Nishida 1979; Wrangham & Smuts 1980), depending on the reproductive state of the female (Matsumoto-Oda 1999). Pepper et al. (1999) discovered that when gregariousness was controlled for, adult males did not associate with each other more often than would be expected by chance, and anoestrous females associated with each other more often than would be expected by chance (Pepper et al. 1999). This suggests that although females are commonly seen alone or in small groups, they have strong associations with particular females (see Appendix 1). Until studies on other populations are completed, or re-analysed, using the same methods as Pepper et al. (1999), it will be unknown if this is the case for all chimpanzee communities.

### **Individual choice**

Although there are many factors that affect association and proximity of chimpanzees, the individual's choice of whom to associate with also plays an important role. In a study of the male chimpanzees from the Budongo Forest's Sonso community, it was concluded that association was the result of tactical decisions, rather than random and passive association, such as meeting at a fruiting tree (Newton-Fisher 1999a).

If chimpanzees choose with whom to travel and associate, then it is possible that injured chimpanzees are less often chosen as association partners, or that injured chimpanzees prefer to associate with other injured chimpanzees.

### **4.3 Aims of this chapter**

The aim of this chapter is to determine whether injured adult female chimpanzees of the Budongo Forest's Sonso community form groups of the same size and composition as non-injured chimpanzees, and to determine how injury can affect their association and proximity patterns.

The hypothesis is that injured chimpanzees will spend more time in smaller groups, as injured chimpanzees may have difficulties keeping up with larger groups of chimpanzees (Ghiglieri 1988). It is also hypothesised that injured chimpanzees will spend more time alone, or in association with other injured chimpanzees, if a lack of tolerance is shown by other community members. These hypotheses would lead to reduced social opportunities for the injured individual, and its offspring, which could affect long-term behaviour patterns.

As many as possible of the factors described above, which have been previously studied and found to affect grouping and association, will be included in this analysis in order to determine how injury alone affects the group size, composition, association and proximity in chimpanzees.

### **4.4 Methods**

#### **4.4.1 Data collection**

Scan sampling was used in order to collect data on the group size, group composition, association and proximity relations of the adult females of the Sonso chimpanzee community (see section 3.4). The number of scans recorded for each of the 12 mothers, and the numbers of actual scans used in the analysis (see section 4.4.3) are given in Table 4.1.



**Table 4.1** Number of scans recorded for each focal subject.

<i>Focal subject</i>	<i>Code</i>	<i>Number of scans recorded during study period</i>	<i>Total scans used in analysis</i>
Banura	BN	93	32
Kigere	KG	107	36
Kalema	KL	123	42
Kewayya	KY	128	44
Zana	ZA	110	39
Injured - total		561	193
Zimba	ZM	128	43
Janie	JN	112	38
Kutu	KU	89	31
Kwera	KW	132	45
Nambi	NB	110	38
Ruda	RD	99	34
Ruhara	RH	86	29
Non-injured - total		756	258
All subjects - total		1317	451

#### 4.4.2 Definition of terms

**Group size:** A group was defined as all chimpanzees visible to the observer, or known by the observer to be present (Newton-Fisher et al. 2000) within approximately 50m of the central point of the group. Only independent chimpanzees are included in the group size count. Dependants include all young chimpanzees between the age categories Infant 1 to Juvenile 1. Juvenile 2 by definition can be in a separate group from the mother (Table 3.4), so are included as independent individuals in this analysis, unless otherwise stated.

Group size was divided into either small or large groups (Reynolds & Reynolds 1965; Wrangham et al. 1992).

Small groups: six or fewer independent individuals.

Large groups: seven or more independent individuals.

**Group composition:** Types of groups formed are classified as follows, and based on Goodall (1986).

- |                         |   |
|-------------------------|---|
| Family unit:<br>(group) | a mother and her dependants, with or without older juvenile and sub-adult offspring (with exception of Zimba and Kewayaya, thought to be mother and daughter, who together with their dependants were classed as a nursery group, keeping the family unit as the most solitary unit for mothers). |
| Nursery group:          | two or more family units, sometimes accompanied by non-related childless females. Also includes one family unit with non-related childless females.   |
| Mixed group:            | one or more adult or sub-adult males with one or more adult or sub-adult females, with or without dependants.   |
| Sexual group:           | mixed group in which one or more of the females is in oestrus.  |

N.B. All-male groups were not included in this study as data were only collected when at least one female and her dependants were present.

**Oestrous females:** Oestrous female refers to females with anogenital swelling of 3 or 4 (see section 3.4.4). It is during this period of anogenital swelling that males are attracted to the oestrous females and most copulations occur (personal observation). This finding is similar to other studies in which periods of semi-swelling are not included in the analysis because copulations are infrequent during this time (Matsumoto-Oda & Oda 1998).

**Group activity:** The behaviour of the group was recorded at each scan. One of the following categories was selected if approximately two-thirds (or more) of the group were engaged in that activity, or associated activities.

Feeding:	feeding behaviours including foraging, feeding, wadging, paying attention to another individual feeding, food sharing, etc.
Resting:	lying in a relaxed manner on the ground or in a tree either in or out of a nest.
Travelling:	moving as a group on the ground or in the trees to a new feeding, resting or other site.
Social:	individuals playing or grooming.
Mixed:	if group members were involved in more than one of the above activities.

### **Association and Proximity:**

Association refers to the individuals that are in the same group as the focal subject.

Proximity refers to individuals that are within a specified distance of the focal subject. In this study the proximity distances are one metre and five metres.

Three different types of relationships, or contexts for a chimpanzee to be in close proximity to another are recognised: friendly, sexual and unfriendly (Goodall 1986). Aggressive interactions are in general short-lived, and also rare amongst females. No cases of aggressive interactions were recorded during scan sampling, and only 30 aggressive interactions involving the females were recorded during focal animal samples. Few of the focal subjects were in oestrus during the study period, so proximity in most cases in this study refers to friendly association.

### **4.4.3 Analysis methods**

The first scan for each observation period was used in the analysis so as to ensure that the data points were independent of each other (see Table 4.1). The first scan was chosen (rather than the second or last scan in the observation period) as focal subjects were never out of sight during the first scan. The number of scans used in the analysis corresponds roughly with the number of focal animal samples (half hour observation periods) recorded on each individual (Table 3.6). For one observation period, focal animal sampling data were available where scan data



were not, and for a second observation period the reverse was true (for focal subjects BN and KL).

### **Group size and composition**

Statistical analyses were conducted using a binomial Generalised Linear Model (see section 3.5). The Bonferroni correction method was used (see section 3.5.2), resulting in a significance level of 0.004; this significance level is used in all analyses unless otherwise stated. Some results have been mentioned that would be significant at the 0.05 level, and although not significant in this analysis, they are included in order to indicate general trends in the data. Significance values are always given in these cases.

Factors included in the binomial GLM were: injury status of the mother, activity of the group, group type (or composition), season, and presence of oestrous females in the group. Differences in grouping patterns already described for each sex are eliminated because only one age/sex class is under consideration in this study. Other factors not included in the analysis, that are known to affect group size and composition (see above), are: food supply, hunting rate and predation risks. Food supply was not recorded during the study, but group feeding behaviour was recorded at each scan as activity of the group. Only two hunting episodes were observed during the study period and data were not being collected during these times. Predation has not been recorded since the beginning of the project 10 years ago, although, as will be discussed later (see section 7.7), it remains possible that individuals still respond, or perhaps group, according to past predation pressure.

### **Association and proximity**

#### **Dyadic Association Index**

The association index used to analyse the data was the Index of Familiarity or Dyadic Association Index (Boesch & Boesch-Achermann 2000; Ghiglieri 1984; Hayaki 1988; Kawanaka 1989; Newton-Fisher 1999a; Nishida 1968; White &

Burgman 1990). This index is a measure of how much time two individuals spent together as a proportion of the amount of time at least one of the individuals was observed. This method has been recently criticised as it overlooks the effects of general gregariousness, which are different for males and females (Pepper et al. 1999). The alternative methods set out by Pepper et al (1999) are difficult to use in the present study, and possibly irrelevant as data were collected and compared between females only (almost always anoestrous), who have the same general gregariousness. Difficulties arise if the association levels seen in this study are compared with other chimpanzee studies (see Appendix 1).

For two individuals (a) and (b) the Dyadic Association Index (DAI) = 
$$\frac{C}{A + B + C}$$

Where:        A is the number of scans were only (a) was in group  
                   B is the number of scans were only (b) was in group  
                   C is number of scans where both (a) and (b) are in group

DAI's could only be calculated for dyads containing adult females, as males and other females were never the focal subject. DAI's were calculated for association (in the same group), then for proximity (within 5 metres of each other). Data were collected for within 1 metre, but dyads spent very little time in this proximity and so the two categories (within 1 metre and between 1 and 5 metres) were combined for this analysis.

Tables of DAI were created and then cluster analysis was used to create dendrograms. Two methods were used to create the dendrograms, the complete link and average link methods (Gordon 1999). The complete link method analyses the distance between clusters by using the maximum distance between any 2 units in those clusters; the average link method uses the average distance between clusters, rather than the maximum distance.

### **Social Time Index**

A further index was calculated to determine when focal subjects were in proximity of at least one other chimpanzee. The social time index (STI) used is similar to

that described by Hayaki (1988), although he looked at when focal animals stay within 10m of at least one individual (Hayaki 1988). In this study STI will be based on the proportion of scans that a focal subject was:

- (a) within 5m of any other individual
- (b) within 1m of any other individual

$$\text{STI} = \frac{\text{Number of scans focal subject within proximity of at least one individual}}{\text{Total number of scans of the focal subject}}$$

Infants and juveniles have not been included in this analysis as they frequently spend time within 1m and 5m of their mother.

### **Closest associate**

The eight closest associates of each of the 12 study females were recorded. This was determined by calculating the number of times a focal subject was in association (in the same group) with each other community member (not including dependants and older juvenile siblings). These other community members were then grouped into separate age/sex categories. The analysis was conducted using data on association only.

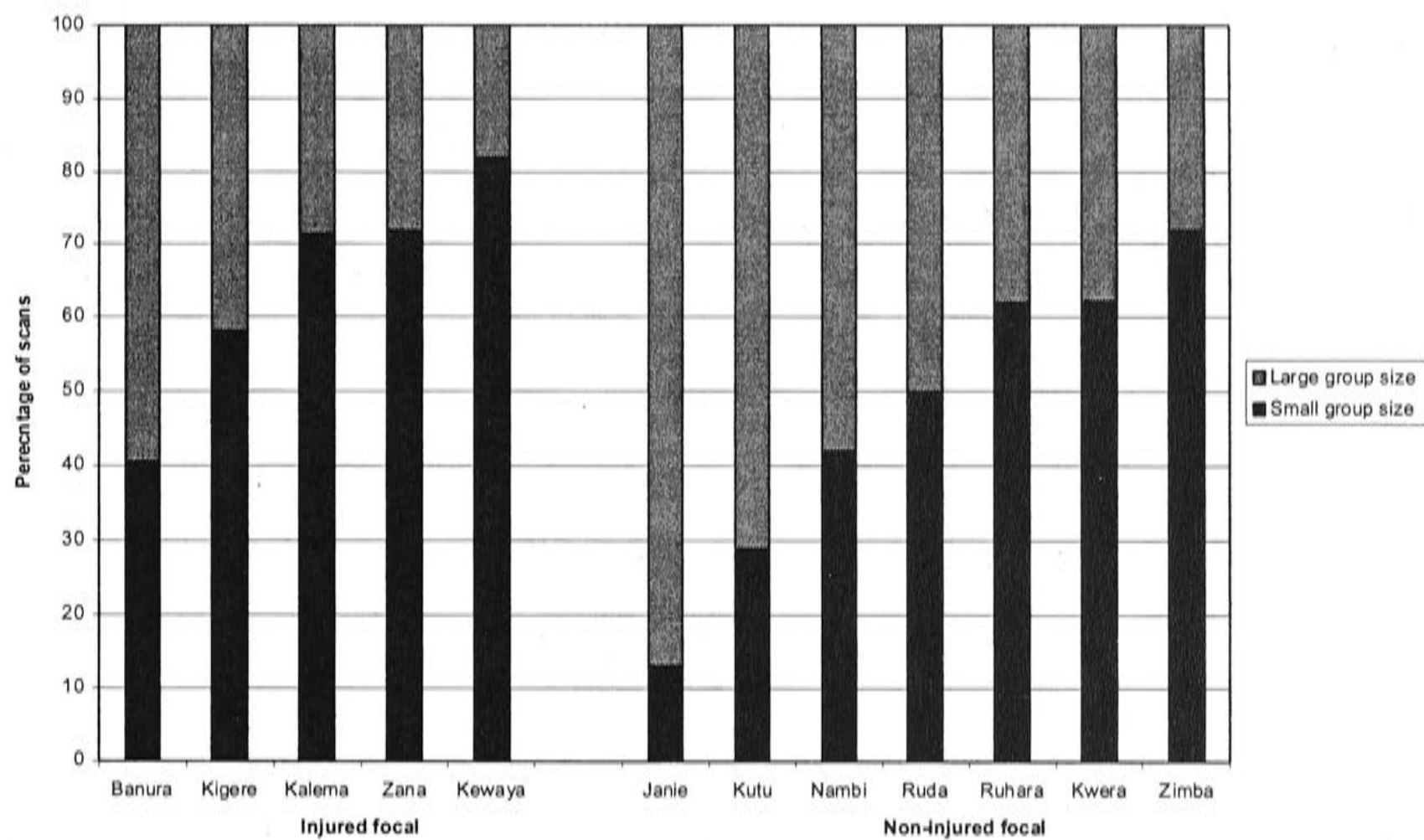
## **4.5 Results**

### **4.5.1 Group size**

Group size was divided into small and large groups for analysis (see section 4.4.2). A total of 252 small groups and 201 large groups were recorded. The percentage of small and large groups for injured and non-injured individuals was calculated and is shown in Figure 4.1. There is a general trend for injured chimpanzees to spend more time in small groups than non-injured chimpanzees.



**Figure 4.1** Group size (small and large groups) as a percentage of total scans for each individual  
(refer to Table 4.1 for number of scans used in analysis)

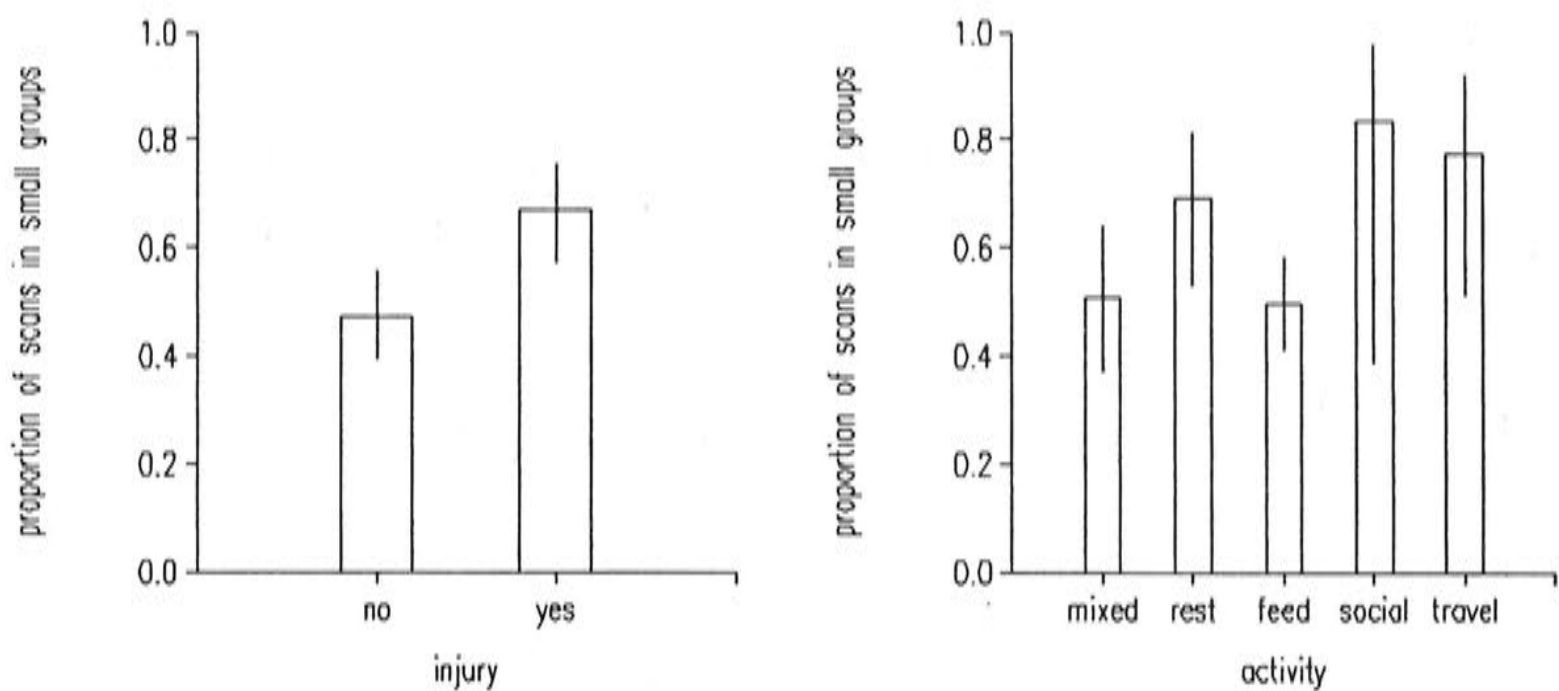


A binomial GLM was used in order to test whether injured chimpanzees spent more time in small groups (as opposed to large groups) than non-injured chimpanzees. When injury status was considered alone it did not significantly affect the size of the group formed ( $F=2.58$ ,  $d.f.=1,10$ ,  $n.s.$ ).

Other factors are known to affect the size of chimpanzee groups. A binomial GLM allows for the testing of the effects of multiple explanatory variables on the response variable (in this case group size). Explanatory variables used in this analysis were group activity, group type, presence of oestrous females and season. Each was considered in turn after adjusting for injury status.

A significant difference was found for injury status across all group activities, injured chimpanzees spent significantly more time in small groups ( $F=9.56$ ,  $d.f.=1,47$ ,  $p=0.003$ ). This is shown in Figure 4.2.

**Figure 4.2** Proportion of scans spent in small groups for injured and non-injured, and across all activity types



Aside from injury status results also showed that the activity of a group affected the size of the group formed ( $F=2.76$ , d.f.=4,47,  $p=0.038$ ). Although not a significant result there was a trend showing that feeding and mixed groups were most often large groups and resting, travelling and social groups were most often small groups.

Group type also significantly affected the size of the group ( $F=78.5$ , d.f.=3,38,  $p<0.001$ ). Nursery groups and family groups were most often small groups, and sexual groups were most often large groups (family units by definition will always be small, as they contain only the mother and her dependants, which are never greater than six). Mixed groups were equally small or large groups.

There was no effect of season on group size formed.

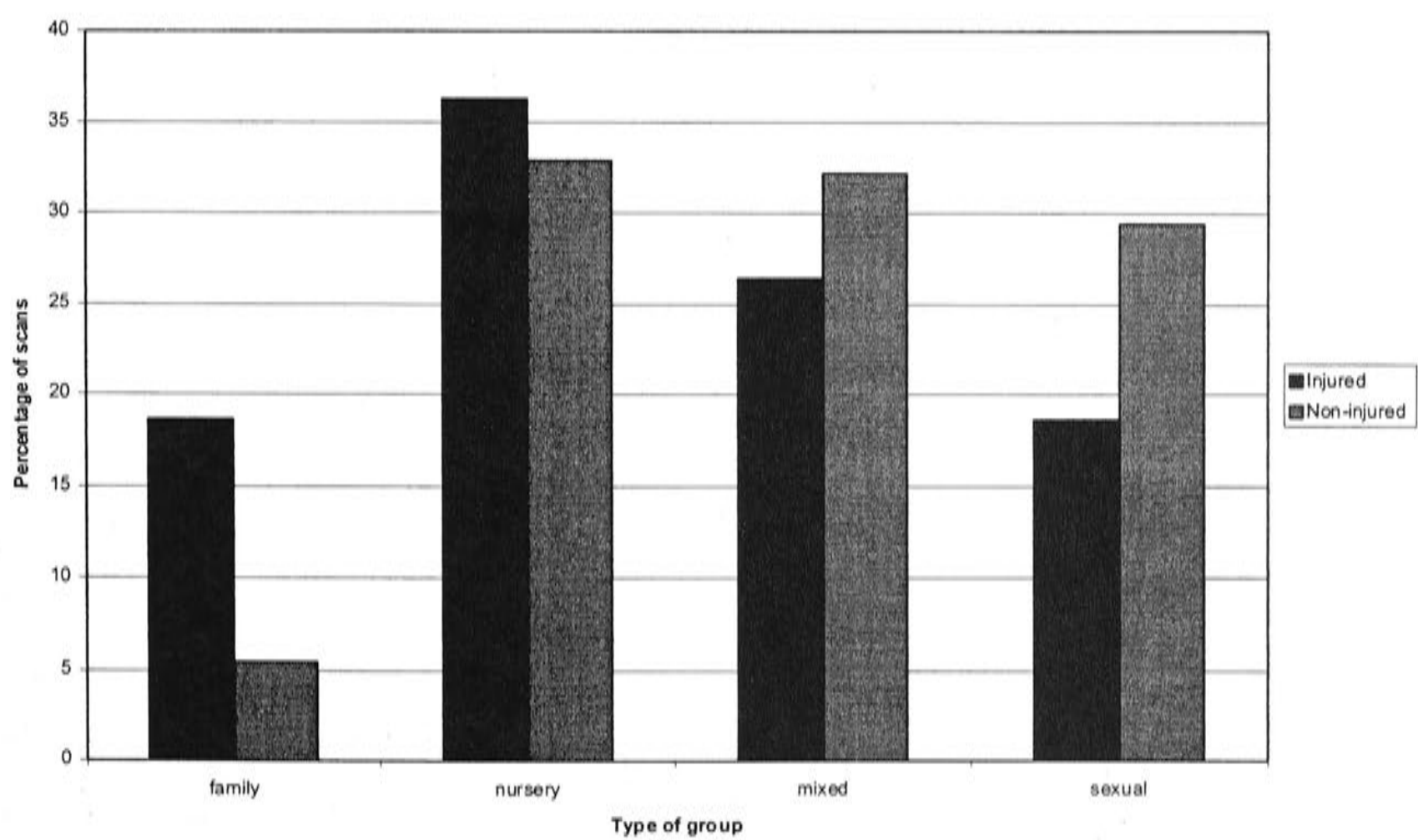
The presence of oestrous females affected the size of the group formed ( $F=39.02$ , d.f.=1,20,  $p<0.001$ ). Groups with one or more oestrous females were most often large groups and groups with no oestrous females were most often small groups. There was no effect of injury status.

These results show that injured chimpanzees spent more time in small groups than non-injured chimpanzees when allowing for the effects that group activity has on the results. Other factors also affected the size of group formed, but did not affect injured and non-injured chimpanzees in significantly different ways.

4.5.2 Group composition (group type)

Percentages of scans in each group composition were calculated by looking at the number of scans either injured or non-injured mothers spent in each group type, and dividing this by the total number of scans where either injured or non-injured mothers were observed. Figure 4.3 shows these results.

**Figure 4.3** Percentage of scans in each group composition type  
(refer to Table 4.1 for number of scans used in analysis – see totals for injured and non-injured groups)



From Figure 4.3 it appears that injured chimpanzees spent much more time than non-injured chimpanzees in family units, and spent much less time than non-injured chimpanzees in sexual groups.



To test this a binomial GLM was used to see whether the injury status of the mother had an effect on the proportion of scans found in each of the four group types. No significant difference was found for any of the group types (family unit  $F=5.78$ , d.f.=1,10,  $p=0.037$ ; nursery group  $F=0.12$ , d.f.=1,10, n.s.; mixed group  $F=0.54$ , d.f.=1,10, n.s.; sexual group  $F=2.45$ , d.f.=1,10, n.s.). Although not significant to the  $p \leq 0.004$  level, the result for proportion of scans spent in family units shows a trend towards injured chimpanzees spending more time in family units than non-injured chimpanzees.

The type of group formed can also be affected by additional factors such as group activity, season and presence of oestrous females. Once again a binomial GLM was used to determine the effects of these explanatory variables on group composition. Each factor was considered separately after adjusting for injury.

Injured chimpanzees spent significantly more time in family units ( $F=14.49$ , d.f.=1,47,  $p < 0.001$ ) across all group activities (see Figure 4.4). A trend was also found whereby injured chimpanzees spent less time in sexual groups than non-injured chimpanzees across all activities ( $F=4.95$ , d.f.=1,47,  $p=0.031$ ); this result was not significant to the  $p \leq 0.004$  level. There was no combined effect of injury and activity.

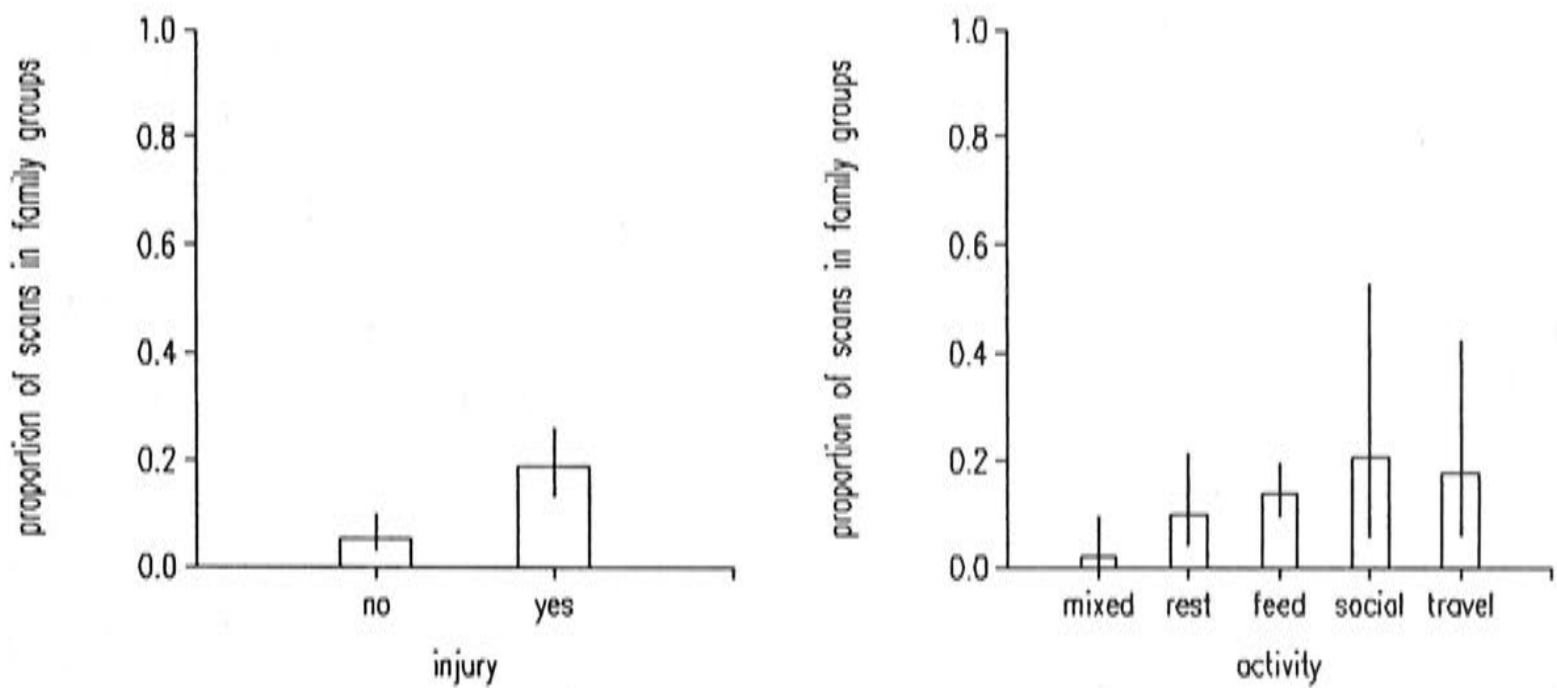
A strong trend was seen for injured chimpanzees who spent more time in family units for both seasons ( $F=9.30$ , d.f.= 1,20,  $p=0.006$ ). There was no difference seen for season for other group compositions.

The activity of the group affects the proportion of scans spent in family and sexual groups. Family units were more often social or travelling groups and less often feeding or resting groups ( $F=3.02$ , d.f.=4,47,  $p=0.027$ ). Very few family units were mixed activity groups (since a mother and her offspring are less likely to be involved in different activities). Although not significant, this result shows a general trend towards the activities most and least common for family units. Sexual groups on the other hand were more often mixed and feeding groups, and less often social, travelling or resting groups ( $F=2.99$ , d.f.=4,47,  $p=0.028$ ). Once

again this result is not significant to the  $p \leq 0.004$  level, but is included here to allow for the general trend to be noted.

Only for nursery groups was it necessary to analyse the effects of oestrous females on group composition. Nursery groups without oestrous females were more common than nursery groups with oestrous females ( $F=22.82$ ,  $d.f.=1,20$ ,  $p<0.001$ ). Family units never contained oestrous females in this study, which is expected since females are more likely to join with males during periods of oestrus. Furthermore only two study females were in oestrus during the study period. Mixed groups contain no oestrous females and sexual groups always contain at least one oestrous female by definition (see section 4.4.2).

**Figure 4.4** Proportion of scans in family groups for injured and non-injured, and across all activity types



These results show that injured chimpanzees spent significantly more time in family units, and generally spent less time in sexual groups, than non-injured females, when allowing for the effects that group activity has on the results. Once again other factors are seen to affect the group composition formed, but injured and non-injured chimpanzees are affected in the same way by these factors.

4.5.3 Proximity and association

The dyadic association indices are shown for all adult females with dependants in Table 4.2 and Table 4.3. The first table shows the association between adult females, the second looks at the proximity between adult females. Association is defined as individuals within the same group; the proximity measure is individuals within 5 metres of each other. In both cases the higher the DAI the stronger the association or proximity between the two individuals. Two letter codes used for female names in Table 4.2 and Table 4.3 can be translated using Table 4.1 earlier in this chapter.

Table 4.2 DAI of association (injured females in bold)

	<b>BN</b>	ZM	JN	<b>KG</b>	<b>KL</b>	KU	KW	<b>KY</b>	NB	RD	RH	<b>ZA</b>
<b>BN</b>												
ZM	.20											
JN	.26	.25										
<b>KG</b>	.17	.25	.19									
<b>KL</b>	.24	.34	.26	.26								
KU	.24	.28	.33	.27	.37							
KW	.17	.31	.25	.29	.39	.34						
<b>KY</b>	.19	.62	.24	.29	.37	.28	.39					
NB	.21	.16	.32	.15	.26	.25	.30	.21				
RD	.35	.21	.25	.24	.23	.22	.24	.21	.18			
RH	.16	.16	.29	.13	.19	.19	.16	.16	.12	.22		
<b>ZA</b>	.20	.12	.21	.11	.18	.23	.21	.16	.16	.15	.18	



**Table 4.3**      DAI of proximity (injured females in **bold**)

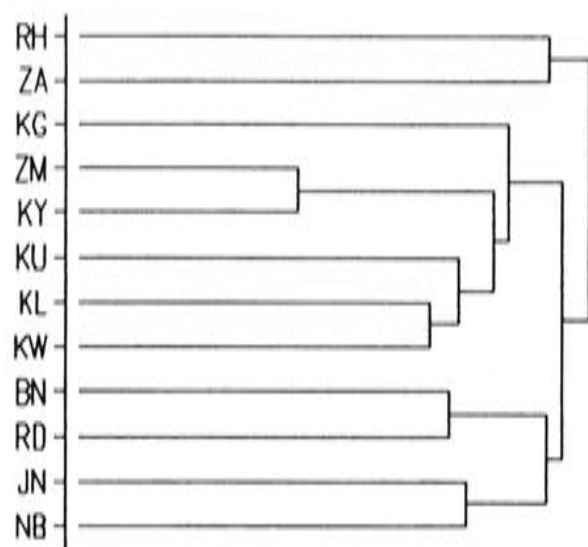
	<b>BN</b>	ZM	JN	<b>KG</b>	<b>KL</b>	KU	KW	<b>KY</b>	NB	RD	RH	<b>ZA</b>
<b>BN</b>												
ZM	.01											
JN	.04	.04										
<b>KG</b>	.01	.09	.01									
<b>KL</b>	.00	.03	.01	.01								
KU	.05	.03	.07	.02	.03							
KW	.04	.05	.04	.08	.13	.06						
<b>KY</b>	.03	.37	.06	.09	.06	.05	.11					
NB	.02	.01	.15	.01	.07	.02	.07	.03				
RD	.05	.05	.03	.06	.01	.00	.07	.03	.01			
RH	.00	.01	.02	.01	.01	.02	.01	.02	.00	.00		
<b>ZA</b>	.00	.01	.00	.01	.02	.02	.02	.02	.00	.00	.00	

Dendrograms were created using cluster analysis from the DAI tables. Two methods were used, complete link and average link, to gain the results shown in Figures 4.5, 4.6, 4.7 and 4.8. In the descriptions below, all injured individuals are underlined.

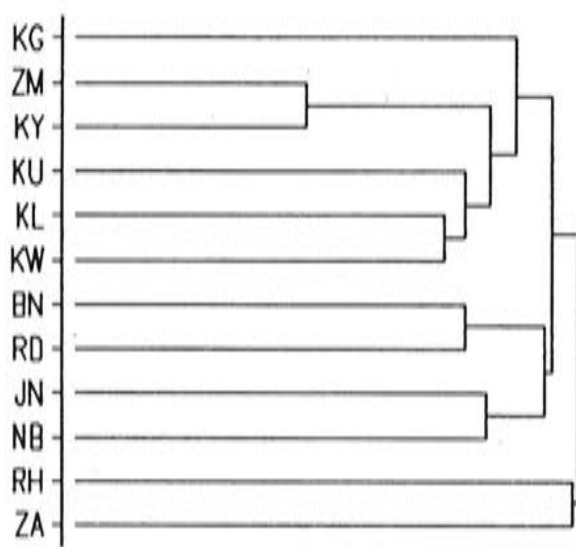
**Association**

The two methods (complete link and average link) give the same result (see Figures 4.5 and 4.6). Ruhara and Zana are the most isolated from the rest of the group. The remaining individuals were divided into two groups: one with two pairs, Banura and Ruda together and Janie and Nambi together, and the other with Kewaya, Kutu, Kalema, Kwera, Kigere and Zimba. Kigere is the most distant from this later group, then the very close pair of Zimba and Kewaya. Kalema and Kwera are also a pair, with Kutu closely linked to that pair.

**Figure 4.5**     DAI of association – complete link method



**Figure 4.6**     DAI of association – average link method



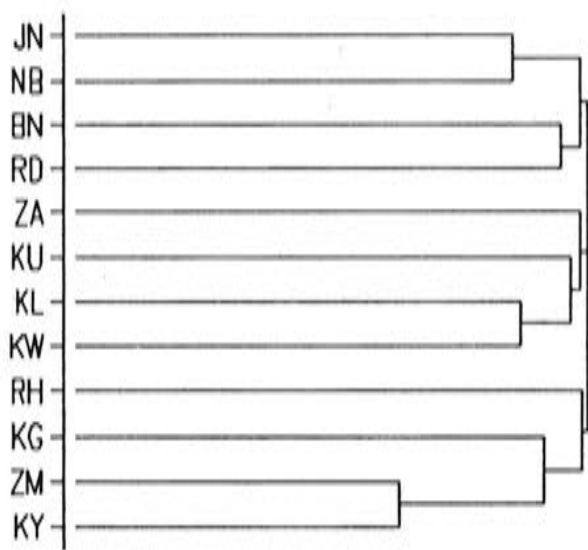
**Proximity**

The two methods in this case revealed slightly different dendrograms (see Figures 4.7 and 4.8). The average link method had similar results to the association data; only Kutu is now grouped with Nambi and Janie, and Kigere is placed closer to the very closely linked Zimba and Kewaya. In the complete link method three groups with equal distance separating them were established. The first has two pairs: Janie and Nambi, and Banura and Ruda. In the second Kalema and Kwera are closely linked, and then Kutu and lastly Zana linked to them. The third has the very close link of Zimba and Kewaya, linked then to Kigere and lastly to Ruhara.

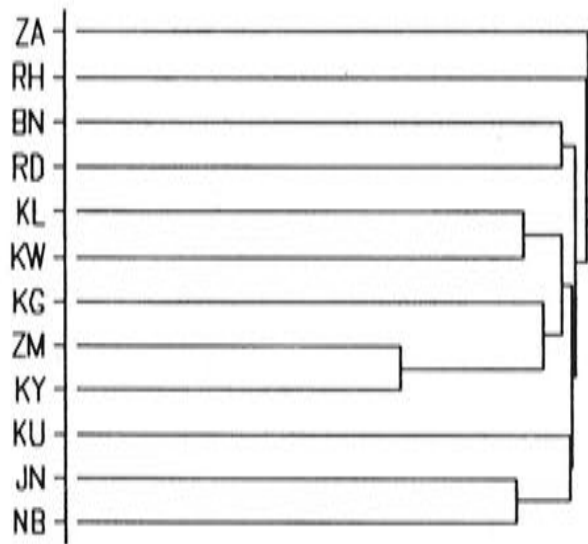
Although these two dendrograms are different, the same pairings came out in each. Always Zimba and Kewaya are the most closely linked, followed by Janie and Nambi, then Kalema and Kwera, and lastly Banura and Ruda (although some further linkages to other pairs are closer linked than this final pair). Other

similarities include the linkage of Kigere to the Zimba / Kewayaya pair, and Zana and Ruhara not being closely linked in either dendrogram.

**Figure 4.7**     DAI of proximity – complete link method



**Figure 4.8**     DAI of proximity – average link method



Both injured and non-injured chimpanzees have both high and low association and proximity levels. The main pairs that are seen in the dendrograms are mixed pairs of injured and non-injured individuals. Of the two individuals that are most loosely bonded to the rest of the females one is injured and the other is non-injured.

N.B. The present study reveals female-female DAI's of levels much higher than seen in other studies (Boesch & Boesch-Achermann 2000; Wrangham et al. 1992). Data were collected only on females in this study, and only groups containing the 12 study females were followed, creating a female bias. In contrast

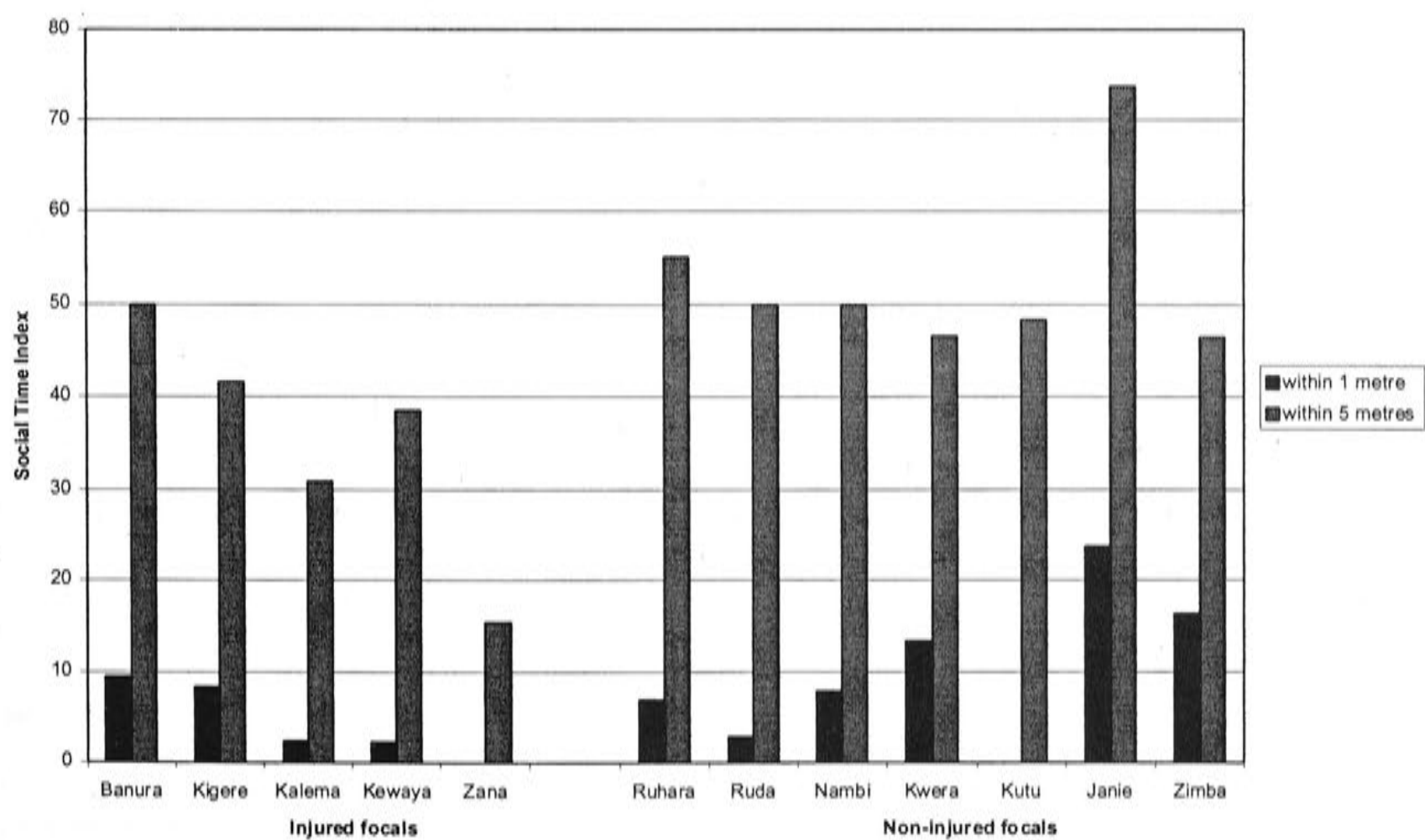


females have been undersampled in all previous field research on chimpanzees (Pepper et al. 1999). For more details on the comparison of the above association data with data elsewhere in the literature, refer to Appendix 1. The important factor in this study is the comparison of injured females with non-injured females, and so the DAI's seen here, although female biased, are appropriate for the focus of this chapter.

### Social Time Index

Social Time Index results are presented in Figure 4.9. This shows that injured chimpanzees spent between 15% and 50% of scans within 5 metres of at least one other individual, whereas non-injured chimpanzees spent between 47% and 74% of their time within 5 metres of at least one other individual. One injured individual, Zana, spent much less time within 5 metres from any other individual.

**Figure 4.9** Social Time Index



The results for STI within 1 metre show less difference: non-injured chimpanzees spend between 0 and 24% of their time within 1 metre proximity of at least one other individual, while injured chimpanzees spend between 0 and 9%.

This result suggests that injured chimpanzees may spend less time within 5 metres of other community members, which is most pronounced for Zana (who has two injuries). There is too much variation between individuals of both categories to determine anything conclusive from the results of 'within one metre of at least one other community member'.

### Close associates

Table 4.4 shows the eight closest associates (not including dependants and older juvenile siblings) of each of the 12 study females. On average, injured females have slightly fewer adult males as close associates, and slightly more adult

**Table 4.4** Eight closest associates of study females by age/sex category

Injured focal subjects	Adult male	Adult female	Sub-adult male	Sub-adult female
Banura	1	5	0	2
Kewayaya	1	5	0	2
Kigere	0	6	0	2
Kalema	1	6	0	1
Zana	1	3	1	3
Mean	0.8	5.0	0.2	2.0
Non-injured focal subjects	Adult male	Adult female	Sub-adult male	Sub-adult female
Zimba	0.33	5.66	0	2
Janie	3	1	2	2
Nambi	3	4	0	1
Kutu	1	5	0	2
Kwera	0	6	0	2
Ruda	1	4	0	3
Ruhara	0.33	4.33	1	2.33
Mean	1.2	4.2	0.4	2.0

females as close associates. The differences are slight, and most likely due to preferences of particular individuals. In particular Nambi and Janie spent more time in association with adult males. As Nambi is the alpha female (see Appendix 2) this would be expected. Janie, who was a very young first time mother, seemed to behave as if she was still a cycling sub-adult, often being one of the first mothers to leave a large group following males, at least in the first few months after the birth of her infant.

#### **4.5.4 Summary of Results**

- Injured chimpanzees spent a significantly greater proportion of time in small groups (as opposed to large groups) than non-injured chimpanzees.
- Injured chimpanzees spent significantly more time in family units than non-injured chimpanzees.
- A trend was seen where injured chimpanzees spent less time (although not significantly) in sexual groups than non-injured chimpanzees.
- The presence of oestrous females significantly affected both the size and composition of the group formed.
- No difference was apparent between injured and non-injured individuals in female-female association and proximity.
- Injured individuals in this study spent less time (although not significantly) within 5 metres of at least one other community member. Individual difference seemed to be the only factor affecting the age/sex class of injured and non-injured individuals' closest associates, as well as the time spent within one metre of at least one other community member.

#### **4.6 Discussion**

##### **4.6.1 Group size and composition**

Injury is seen to have a significant effect on the size and the composition of groups in which adult female chimpanzees of the Sonso community are members. This is apparent when activity of the group was included as a factor in the



analysis, which supports the idea that many factors affect both group size and composition (as described in section 4.2).

Party size has been seen to vary significantly with group activity in an earlier study at Budongo that focused on male behaviour (Newton-Fisher 1999a), and in the current study both group size and composition vary for each activity type. Studies from other field sites also reveal that activity of the group affects the size of the group formed (Boesch & Boesch-Achermann 2000, for example).

The results show that injured chimpanzees spent more time in small groups and family groups than non-injured chimpanzees. In this study family units by definition are always small groups, whereas small groups may be family, nursery, mixed or sexual groups. Injured chimpanzees may spend more time in small and family groups because: they cannot keep up with larger groups, they are socially isolated from larger groups, in order to reduce feeding competition, or because they prefer to be in groups such as family and nursery groups which are commonly smaller in size.

### **Keeping up with large groups**

Sexual groups were most often large groups, and nursery and family groups were most often small groups. Sexual groups contain adult and/or sub-adult males, whereas nursery and family groups do not (excepting sub-adult offspring in family groups). Males have been found to have longer day ranges than females, and to travel faster than females (Wrangham & Smuts 1980); they also range more widely than females, visiting the boundary areas of their territory (Goodall 1986). It would seem that larger groups of a mixed or sexual nature, containing many males, would travel longer distances than smaller nursery or family groups. This was found to be the case in a study from Gombe National Park, with males travelling further per day when parties were larger (Wrangham & Smuts 1980). Injured females have a stronger tendency than non-injured females to remain in small and family groups; perhaps they choose to spend time in such groups to reduce the distances they need to travel, or perhaps they have little choice, as they cannot keep up with the pace of a large travelling group. Results discussed later in

this thesis support these ideas, as more severely injured chimpanzees are found to spend less overall time moving (see Chapter 7).

Anecdotal observations also support the idea that injured chimpanzees may not be able to keep up with larger groups. As mentioned earlier, Ghiglieri (1988) describes a large travelling group of chimpanzees at Kanyawara, Kibale Forest, moving a long distance to a fruiting tree. He observed two small groups of chimpanzees breaking off from the main group. One group consisted of two injured chimpanzees, the other a family unit in which the juvenile daughter had a wire snare around her wrist. These individuals were thought to be isolated because of their injuries and this was seen as an example that "such wounds could have ... serious social repercussions" (Ghiglieri 1988, p.179). There were many occasions in the present study when it seemed obvious that injured chimpanzees were staying behind when a large travelling group moved off, or when injured individuals were travelling alone. When a large fruiting tree was ripe, groups of the community would gather to feed, and after a while begin to disperse. Zana, on many occasions, was the last remaining chimpanzee at the site, and would remain there feeding for many hours (see description at the beginning of this chapter). For example on 1<sup>st</sup> December 1999 a large mixed group of 20 adult and sub-adult chimpanzees were observed feeding on *Ficus natalensis* at 07.33 hours. By 09.57 Zana and her juvenile were the only remaining individuals; they remained in the tree feeding until 16.54. On another occasion (5<sup>th</sup> February 2000), when a large group were gathered, all individuals except Zana and Kigere (both injured), responded to loud calls in the distance by moving off towards them. On yet another occasion (8<sup>th</sup> January 2000), when Zana was seen travelling with a large group, she was one of the last to leave the feeding site, and then broke off from the travelling group to travel alone. She arrived at the next feeding site 15 minutes later than the others in the group. Furthermore, as mentioned above, the most severely injured chimpanzees in this study (Zana and Kigere) spent less time moving than did less or non-injured chimpanzees (see Chapter 7).

If difficulty in keeping up is the reason why injured chimpanzees spent more time in small and family groups it may seem plausible that injured chimpanzees would spend more time with other injured chimpanzees, who may travel at a similar



speed. The data on association and proximity indicate that this was not the case; no two injured adult female chimpanzees were linked to each other more closely than to a non-injured adult female chimpanzee.

It is also possible that a greater uncertainty exists in a large mixed-sex group. An individual has less control over decisions that are made about when to travel off to another feeding or resting site, and over the speed of travel of the group. It is more likely that one or two other chimpanzees will wait for an injured individual, if they do have difficulty keeping up, whereas it is possible that a large mixed travelling party are less likely to be aware of the needs of an individual. More data are required on travelling groups to determine if this is the case.

These results support the hypothesis that injured chimpanzees spend more time in small and family groups because they have difficulty keeping up with large travelling groups. Large travelling groups more frequently include males, who tend to travel faster and further, and may be less responsive to the speed of lagging individuals.

### **Socially isolated from large groups**

The question of lack of tolerance from other group members is difficult to measure. Tolerance can be measured by observing aggression – as tolerance increases, the severity of aggression decreases (Sterck et al. 1997). In the present study there were not enough data on aggressive interactions involving the study females to determine whether this was the case (only 30 events recorded during the study period). In general, aggression is difficult to measure between adult females since they are involved in dominance interactions far less frequently than males, even in captivity where females are in closer contact (Baker & Smuts 1994). Tolerance here has instead been measured by determining the association and proximity relationships of female chimpanzees: a closer proximity reflecting greater tolerance. There seems to be no difference between injured and non-injured chimpanzees for proximity and association to other adult females, which suggests that injured chimpanzees are not socially isolated from other group members (at least from other females), indicating a degree of tolerance. In



addition, ad-lib and informal observations of injured and non-injured chimpanzees support the idea that injured chimpanzees are well tolerated by other group members. This is supported by data from an earlier study at Budongo that focused on the social integration of disabled individuals; no significant difference for the representation of injured versus non-injured individuals was found (Quiatt & Reynolds 1994).

Zana, the chimpanzee with two injuries, does appear to be socially isolated from other group members in this study, but this may have more to do with her travelling independently more often rather than from any lack of tolerance. She does not receive aggression from other community members when she joins larger groups, and has been observed in grooming interactions (although rarely). The hypothesis that injured chimpanzees' social grouping may be affected by a lack of tolerance from other community members is not supported here.

### **Reduce feeding competition**

Adult female chimpanzees have been described as having a solitary nature, which is thought to minimise the effects of feeding competition (White & Wrangham 1988; Wrangham & Smuts 1980). Injured chimpanzees may spend more time in smaller groups to reduce feeding competition further. Although injured chimpanzees did not spend more overall time feeding when compared to non-injured chimpanzees (see section 7.6.4), the results in this chapter show that they spent more time in small groups when feeding than non-injured chimpanzees. This would have the overall effect of reducing the competition for available food for injured chimpanzees, as the smaller the group size the less competition there is for available food. It is then possible that the sole reason injured chimpanzees spent more time in small groups was so they could feed in small groups. This could then lead to them being more likely to travel, rest, groom and play in small groups.

That feeding competition is a major factor involved in grouping for the study females is further supported by the examples given previously of injured females waiting behind in fruiting trees while other community members move on.

### **Preference for group type**

It may not be that injured chimpanzees prefer small groups, but rather that they prefer particular group compositions. Injured chimpanzees were found to spend significantly more time in family units and less time in sexual groups (although not significantly in the later case). A family unit is the smallest group for mothers, while sexual groups are the most social (sexual groups were most often large groups). The reasons why an injured chimpanzee may choose to travel in a family unit are to reduce feeding competition and to have the flexibility to travel at their own speed. The costs of travelling in a family unit are the reduction in opportunities for social interactions and an increased risk of predation or infanticide. Zana is the most obvious example in this study of an injured individual who spent a great deal of time in isolation; feeding, travelling and resting with only her juvenile male offspring for company.

It is difficult in this study to determine whether injured chimpanzees spend more time in small groups, which results in their spending more time alone, or whether they spend more time in family units and so are commonly seen in small groups. Either way the consequences are much the same (see below).

### **Other factors**

Other factors known to have a strong impact on the formation of groups are presence of oestrous females, hunting, and predation (see section 4.2.1).

During the study period only two of the study females were in oestrus. One became pregnant and had irregular swellings that never reached maximal tumescence (Kalema). The second female cycled regularly throughout the study period (Nambi). She was the alpha female so she commonly spent time in larger mixed and sexual groups regardless of her oestrous state. Therefore the oestrous cycles of the study females did not have a large impact on group formation during this study period. Other nulliparous females in the community were in oestrus, and this did affect group size and composition, although not differently for injured or non-injured chimpanzees.

For this study the effects of hunting and predation are too rare to enable analysis of their effects on group size and composition.

Feeding competition and difficulty in keeping up seem to be the most likely causes of injured chimpanzees spending more time in both small groups and family units. Whether injured chimpanzees choose to be in smaller groups, or are forced to do so by the choices of others because they have difficulties in keeping up, or with competition for food, is difficult to tell from this study. That injured chimpanzees do spend more time alone and in small groups has the potential to impact seriously on both their own and their offspring's social opportunities, and survival (see below).

#### **4.6.2 Proximity and association**

As already mentioned, injury seems to play no obvious role in choice of association and proximity amongst the Sonso females. Zana, with two injuries, seems isolated from all other mothers, although not to any greater extent than Ruhara, who is not injured. All of the closest groupings seen are between an injured and a non-injured, or between two non-injured individuals, never between a pair of injured mothers. The two closest associates seen in all dendrograms are Zimba and Kewayaya, who are thought to be mother and daughter; kin are known to spend time in close association, especially mothers and adult daughters who do not emigrate (Goodall 1986). It appears from these results that injured individuals are well integrated into the social dynamics of females in the Sonso community.

Of the other factors discussed earlier in this chapter that are known to affect the association levels and proximity of chimpanzees (see section 4.2.2), the relationship between kin is the only one to have been mentioned in this section. Other factors included age, sex, social rank and individual choice. All females in this study are from the same age/sex class (and all have dependants), a selection deliberately made to reduce the natural variation found in behavioural data of this kind. Social rank differed among the mothers; Nambi was the highest ranked, which affected her association as she was seen to spend more time with adult



males. Rankings amongst the other 12 females were less obvious (see Appendix 2). Individual choice may certainly be occurring, since females were found to be in closer association with some particular mothers in all analyses above.

It was hypothesised that the association patterns of injured females may be affected if a lack of tolerance was seen from non-injured community members, but this seems not to be the case, at least for females in this study.

How well injured females are integrated with other community members remains an interesting question. The Social Time Index and the data on closest associates allow some insights into this question, from the perspective of adult females. Data from the Social Time Index revealed that non-injured chimpanzees appeared to spend more time within five metres of at least one other individual in the community. This suggests that injured chimpanzees may be less integrated into the rest of the community, but is more likely to be a result of injured chimpanzees spending more time in small groups (as seen above), so having fewer social opportunities. Data on closest associates did not suggest any clear difference between injured and non-injured in their choice of partners by age/sex category; this is not in accord with the idea that injured chimpanzees are less integrated into the rest of the community. Clearly such data are at best suggestive, and more data are required on both males and females, of all age categories, to understand the relationship between injured individuals and the rest of the community.

#### **4.6.3 Possible long term implications**

From these analyses it does not appear that injured females are socially isolated owing to a lack of tolerance shown other community members. While injured females are tolerated when in association with other community members, it is clear that they are still socially isolated to some extent, because they spend more time in small groups and more time alone with their offspring. This is most likely because of increased feeding competition and difficulties in keeping up with travelling parties. Female chimpanzees are known to be semi-solitary in nature (White & Wrangham 1988); it has been shown here that injured females are even more solitary than non-injured females. Both the increased time spent alone, and

the resulting reduction in social opportunities for both injured mothers and their offspring, could have long-term implications.

Time spent alone could increase the likelihood of infanticide and predation, which has implications for the survival of injured chimpanzees and their offspring. Two cases of infanticide have been described for the Sonso community (Newton-Fisher 1999b); one has been described in detail and involved an attack on a lone unknown female and her small infant. In the present study two instances were observed in which members of the Sonso community were carrying a small infant, thought to be snatched from a neighbouring community (the attacks were not observed). In the first case the infant was alive, and was carried by an adult male (Notman & Munn 2003), in the second case the infant was dead and was carried by a juvenile male, an adult female, and an adult male (personal observation). The infant was not observed to be eaten in either of these two cases, rather carried until it began to decay (personal observation). So it may well be that females that spend more time alone, and away from the protection of males, might risk losing infants to neighbouring males. Predation by large carnivores has not been recorded for Budongo chimpanzees (see Chapter Seven for more details), although historically leopards were found in the forest (Reynolds 1965), so it is not impossible that predation may still occur.

A reduction in social opportunities, because of time spent alone, may lead to: a lowering in dominance rank, a lower reproductive rate of the mother, and fewer opportunities for social play for their offspring.

Dominance rank has been described elsewhere in chimpanzees and other primate species to be both affected and non-affected by injuries (see section 2.2). Injured females in the present study are both high and low ranking, although dominance was difficult to determine because there were relatively few female-female interactions (see Appendix 2). If dominance was affected by injury status, this could have implications for aspects such as access to food, association patterns and reproductive success (Pusey et al. 1997).

Reproductive success has been shown to be affected by dominance. In a study at Gombe National Park, high ranking females proved to have higher infant survival and faster maturing daughters, live longer themselves, and produce young more rapidly than lower ranking females (Pusey et al. 1997). Other factors can also affect the reproductive success of individual females. For example, Williams et al. (2002) found that females at Gombe in the northern section of their range had a higher reproductive success than females found in the south, and peripheral females varied in their success. It would seem possible that injury status could also affect reproductive success, or affect ranging patterns, which in turn could affect reproductive success. A study focusing on ranging patterns of the female chimpanzees of the Sonso community revealed that there was no obvious relationship between core area size and the female's position in the dominance hierarchy, nor was there any relationship between female home range size and age of the female (Fawcett 2000). Data are not available on the differences between injured and non-injured females for ranging patterns, nor are data available for inter-birth intervals; both could be used as an indicator of reproductive success. These factors could be determined from long-term studies of the females at Budongo.

More information is also required from Budongo during times when females are in oestrus. As only two study females were in oestrus during the study period (one injured, one non-injured), it is difficult to say whether injured females remain in small and family units when in oestrus, or spend these times in larger mixed groups and have the same sexual opportunities as other females. Since all injured females have successfully reproduced since their injury, it seems likely that they do spend more time in larger groups when in oestrus; also all females in this study spent at least some of their time in large groups of all compositions.

Another repercussion of spending more time in small or family groups is the reduced level of social interactions for young chimpanzees. Infants of injured mothers at Sonso played more than infants of non-injured mothers, but juveniles of injured mothers played less than juveniles of non-injured mothers (see Chapter 5). This seems confusing; in theory it would be expected that if injured mothers spent more time alone and in small groups, then these infants would have less



opportunities for social play. In a study on captive chimpanzees it was also unexpectedly found that more sociable chimpanzee mothers had infants that spent less time in social play (Hemelrijk & de Kogel 1989). While infants remain somewhat of a mystery (for more discussion see Chapter 5), juveniles do seem, perhaps because of their mothers' unsocial nature, to have fewer opportunities for socialisation. An unsocial upbringing could lead to social problems as a sub-adult and adult; for example Zana's sub-adult son Bwoba is very low ranking amongst the males, and shows little sign of confidence, often travelling as the very last in large groups (personal observation). Injured mothers may also have reduced social opportunities because they spend more time alone. There is no difference for the time spent, or the probability of being groomed, by other community members for injured and non-injured chimpanzees, but injured mothers were involved in mutual and group grooming less frequently (see Chapter 6).

#### **4.7 Conclusion**

What is most conclusive from this chapter is that injured adult female chimpanzees with dependants spent more time in small groups, and alone with their dependants, than did non-injured females with dependants. This does not seem to be because of a lack of tolerance shown by other community members. Non-cycling adult females are already known to spend more time alone with their dependant offspring than males (Wrangham & Smuts 1980). It appears here that injured females are even more greatly affected by factors such as feeding competition, which cause females to group in these ways. Injured females also have difficulty keeping up with large groups – whether because of their physical disability or because they choose to stay behind and travel alone. Regardless of the reasons, injured chimpanzees are spending more time in small groups and alone with their dependants, and so have reduced social opportunities. Therefore it seems probable, as Ghiglieri (1988) suggests, that chimpanzees are not only being mutilated and dying from snares but are also suffering from altered social interactions. We need more information from periods when females are in oestrus to determine whether injured females have the same sexual opportunities as non-injured females, and more long term data is needed to assess reproductive success

– data such as inter birth intervals, infant survival, and age of offspring at sexual maturity.

## Chapter Five

### The impact of injuries on free-living chimpanzees – mother-infant relationships

*Late in the afternoon, after many hours feeding alone in a Ficus natalensis, Zana, an adult female with two injured hands, and her juvenile son Zalu were beginning to move high up in the canopy in order to descend to the rainforest floor and move on to find a good nesting tree for the evening. Zana began moving first, slowly as she was walking along the thinner branches at the outer edges of the fig tree. Zalu quickly finished eating and scrambled towards Zana. He climbed onto his mother, who turned and pushed him aside. Zalu tried a second time, and once again he was pushed aside. Zana continued travelling in the tree, reaching larger, more stable branches, at which point Zalu climbed onto his mother again. This time Zana let him stay, and then continued to carry him, stopping occasionally for a few final figs, until they reached the ground and quickly disappeared into the undergrowth. (Budongo Forest: March 2000)*

#### 5.1 Introduction

The mother – infant bond is a crucial part of the development of young chimpanzees. All primate infants are born in a relatively helpless state, compared to other mammals, and are therefore dependent on their mothers for long periods of time (Nicholson 1987; Watts & Pusey 1993). Infants learn both social and survival tactics from their mother, as well as being protected and cared for. Inappropriate maternal behaviour can have implications for the later, adult behaviour of the offspring. Studies on social deprivation in infant primates show that, as they grow older, these infants have less complex and less numerous relationships than non-deprived peers, which can affect reproductive success (Dunbar 1988). Inappropriate maternal behaviour can be linked to illness in young chimpanzees; for example, two infants became sick after stress resulting from the exceptionally high role they had to play in maintaining the proximity between themselves and their mothers (Rijt-Plooij & Plooij 1988). In extreme cases, where



the mother dies, infant chimpanzees can also die; for example at Gombe all infants orphaned below the age of 4 years died within two years of their mothers death (Pusey 1983). Injuries to the limbs in chimpanzees may reduce the maternal support an injured mother is able to give her offspring; this may then have implications for the behaviour, social opportunities, and the development of their offspring.

It has been seen in Chapter Two that primates with injuries are able to raise young successfully, the most outstanding example being Mozu, the Japanese macaque who raised five offspring despite lacking both hands and feet. The injured chimpanzees in this study have also raised many offspring. Rather than looking at infant survival, this chapter looks at behavioural impacts on dependants owing to the possible difference in maternal support given by the injured mothers. For example, mothers with injuries to hands or feet may have difficulty either carrying or grooming their infants; if an injured mother is unable to carry her infant, or carries her infant less than a non-injured mother, it is possible that this could affect the development of the infant, especially during the first few years of life, but may also have consequences later in life. Since injured mothers spent more time alone with their dependants (see Chapter 4), this may give their dependants fewer opportunities for social interactions such as playing, grooming and spending time in close association with other group members. Also other individuals such as mothers, sub-adult females or siblings may spend more time caring for dependants of injured females if they are unable to care for them sufficiently themselves. This could result in the dependants of injured mothers spending more time away from the mother.

This chapter firstly describes infant chimpanzee behaviour and development, and outlines the aims. The remainder of the chapter investigates the effect injury has on the behaviour of both injured mothers and their dependants.

## **5.2 Infant chimpanzees**

### **5.2.1 Stages of young chimpanzee development**

A newborn infant chimpanzee is completely helpless and dependent on its mother (Rijt-Plooij & Plooij 1988); it is supported completely, and able to grip onto the mother fairly well only by the end of the second week (Goodall 1967). By 11-15 weeks the infant begins to crawl about on the mother, and tries to push itself away by grabbing at twigs and leaves (Goodall 1967). It is around 16-24 weeks that most infants break physical contact with their mother for the first time (Goodall 1967).

A chimpanzee infant is carried by its mother from birth until just before its younger sibling is born; infants less than one year are mostly carried ventrally, and those older than one year mostly carried dorsally (Hiraiwa-Hasegawa 1990a). Independent travelling is not common in an infant until about 2 years of age, and even then the mother carries the infant far more than it walks by itself. Between the ages of 2 and 3 the infant is carried about the same amount of time as it walks; after 4 years of age the young chimpanzee walks independently more than it is carried by its mother (Hiraiwa-Hasegawa 1990a).

In the first six months the amount of time spent suckling is greater than in any other time period, although nipple contact is observed until the fifth year (Hiraiwa-Hasegawa 1990a). During the first four months of life infants are not observed to eat any solid food (Hiraiwa-Hasegawa 1990a). It is during the period between 6 months and 1 year that infants begin to eat solid foods (Goodall 1967). Between the ages of 2 and 3 ½ the proportion of solids eaten increases greatly, and the diet of the infant over this time becomes very similar to the diet of the mother (Goodall 1967). Food sharing between mother and infant is most common in the infant's 1<sup>st</sup> and 2<sup>nd</sup> years (Assersohm & Whiten 1999). Until the 2<sup>nd</sup> year of life the mother provides 20% of the infant's total solid food intake, whereas after the 2<sup>nd</sup> year shared food accounts for only 2 – 5% of the total intake (Hiraiwa-Hasegawa 1990b). Food sharing allows young chimpanzees to access foods that are difficult to process, and to learn the necessary processing techniques.

Infants are weaned between the ages of 4 and 7, with a mean of 5 years, 2 months for infants at Gombe National Park (Pusey 1976). After weaning, most young chimpanzees continue to travel with their mothers for a few more years. The time that a chimpanzee leaves its mother is influenced by different factors for each sex. The female begins to travel with adult males when she begins cycling. The average age at the time of first full anogenital swelling for 8 young females at Gombe National Park was 10.8 years (Wallis 1997). At this point females will begin to spend time in neighbouring communities, either transferring permanently or returning to the natal community (Pusey 1983). Around 50% of females at Gombe have been observed to emigrate permanently (Pusey et al. 1997), where at Tai, 95% of adolescent females transfer to other communities (Boesch & Boesch-Achermann 2000). Male chimpanzees on the other hand stay in their natal communities, so the time at which they leave their mothers is more variable. Generally young males reach puberty at around 7 years and from this point onwards begin to move around with their mothers less and less (Goodall 1967). Some males, as they get older, only occasionally associate with their mother, although in one case in Gombe National Park, a male associated with his mother more than with any other female until her death when he was about 20 years old (Pusey 1976).

### **5.2.2 Proximity of mother and infant**

The proximity between the mother and her infant has been studied in both wild and captive settings. The same general trend of changes over time of mother-infant distances was found for both wild and captive chimpanzees (Silk & Kraemer 1976). During the first few months, infant chimpanzees remained in physical contact with their mothers at all times. This gradually declined, with infants spending less time in contact with their mothers, and then it stabilised at around 30% contact time when the infant was around 2 years old (Silk & Kraemer 1976). The comparison between wild and captive infants showed that among the captive group the rates of change in proximity were significantly faster but the break of contact from the mother occurred consistently later for the captive group (Silk & Kraemer 1976). A further study, focusing on the study community in the



Budongo Forest, also found that the physical distance between the mother and her infant changed during the development of the infant; younger infants spent a significantly greater amount of time in physical contact with the mother than older infants (Assersohm 1999). Another study looked at the association partners of young chimpanzees in Mahale Mountains National Park, and found that association indices were higher between mother-daughter pairs than those between mother-son pairs, and both tended to decrease with age (Hayaki 1988).

As stated above females tend to associate frequently with their mothers until they emigrate from the natal group (although some do not transfer, and so stay in close association with their mother), whereas male offspring begin to leave their mothers earlier to spend time with adult males, but still occasionally associate with their mothers since they stay in their natal group. The decline in association between the mother and the infant seems to be due to the growing conflict in the social requirements of each individual, rather than any conflict between them (Pusey 1983).

### **5.2.3 Social behaviour of the infant**

The development of social behaviour is another important part of the life of a young chimpanzee. Aspects of social behaviour discussed here are grooming behaviour, play behaviour, and associating with individuals other than the mother.

In captivity, while the amount of social behaviour between the mother and the infant remains relatively stable from birth to 4 years, the infant undergoes major changes in the amount of time it spends in social activities with others. At around 6 months and at around 18 months of age the infant sharply increases the amount of time spent in social activities with others (Horvat & Kraemer 1981).

In the wild, chimpanzees live in a fission-fusion society, so that there is an opportunity for social encounters with all members of a community. Despite this, some chimpanzee mothers spend a large proportion of their time alone. At Gombe National Park, each adult female with dependent offspring spent 65-70% of their time foraging alone with their offspring (Pusey 1983). Therefore the amount of

social opportunity available to the infant largely depends on the mother's social behaviour; an increase in the time a mother spends alone reduces the chances for the young chimpanzees to associate with others (Hayaki 1988).

Other factors that affect the social behaviour of the mother and therefore may impact on the social opportunities of the infant include the social position of the mother, her oestrous state (Matsumoto-Oda 1999), the maternal style of the mother (some mothers being more restraining and others being more rejecting) (Hemelrijk & de Kogel 1989), and the presence of older siblings (Brent et al. 1997).

### **Play**

Chimpanzee infants experience their first play bouts with their mothers. Mothers tend to play gently with infants by tickling or nuzzling for short periods, until the age of 6 months when infants begin to respond with play face and laughing. At this point the play bouts become longer (Goodall 1986). Play is most common in younger individuals, and play behaviour decreases with age in both male and females (Hayaki 1985). While play becomes less frequent during adolescence, it does persist into adulthood (Goodall 1986).

### **Grooming**

The development of grooming behaviour between a mother and her offspring appears gradually and becomes more frequent as the offspring gets older (Goodall 1968). The earliest age an infant begins grooming its mother is around 10 months (Nishida 1988), with infants less than 2 years of age grooming for no more than 1 minute (Goodall 1968). After the 4<sup>th</sup> year of life substantial amounts of grooming occur. Older adolescents groom their mothers for almost the same amount of time as they are groomed by them (Nishida 1988).

The amount of time that a mother spends grooming her infant differs between study sites. At Budongo, a mean of 87% of a mother's total grooming time was directed towards their infants, and a mean of 19% of total grooming time was



directed at juveniles (Assersohm 1999). This corresponds to 12.2% of total time spent grooming infants and 2.7% of total time grooming juveniles. At Gombe, mothers spend about 5% of total time grooming their unweaned infants (Pusey 1983). Further, a study at the Mahale Mountains reports that the proportion of time that a mother allocated to grooming offspring increased with the number of offspring (Nishida 1988). Most mothers who had 2 or more offspring spent over 80% of their grooming time grooming them, whereas mothers with only one offspring gave between 33 and 54% of their grooming time to their offspring (Nishida 1988).

Infants begin grooming individuals other than their mother around the age of 2 years, but it is not until the end of the fifth year that an infant grooms individuals other than its mother for more than two minutes (Nishida 1988).

### **Interactions with individuals other than mother**

In order to develop sound social behaviour skills, infants need to spend time with individuals other than their mother (Hemelrijk & de Kogel 1989). As suggested above, it is often the mother (her sociability, her status and her oestrous state) that influences the number of social opportunities for a particular infant. Two separate studies have looked into the behaviour of infants with individuals other than the mother; the first discusses alloparental behaviour and focuses on nulliparous females (Nishida 1983), the second discusses the influence of siblings (Brent et al. 1997).

Alloparental behaviour (the handling of smaller infants by individuals other than the mother) is seen in wild populations of chimpanzees, as well as numerous other primate species (Nicholson 1987). In chimpanzees, nulliparous females (both related and unrelated) show the longest bout lengths, and initiate interactions with infants more often than males do (Nishida 1983). Related nulliparous females (i.e. sisters) were seen to take infants from mothers more often than unrelated nulliparae, and were less likely to groom the mother before taking the infant (Nishida 1983). The average distance kept from the mother once the infant was with the alloparent was greatest for unrelated nulliparae, least for adult males, and



intermediate for sisters (Nishida 1983). Benefits of alloparental behaviour include 'learning to mother' for nulliparous females; getting in favour with the mother for adult males; protection and teaching for the infants; and extra feeding and leisure time for the mother (Nishida 1983).

A sibling can provide many benefits to the social development of the infant and, next to the mother, it is probably the infant's most frequent social partner (Nicholson 1987). In a study of 17 wild infant chimpanzees at Gombe National Park the presence of older siblings did influence the social interactions of the 17 infants. The total amount of time spent in social interaction was similar for infants with and without siblings, but infants with siblings spent more time socialising with their siblings, whereas those without siblings socialised with other group members (Brent et al. 1997). Interactions with the mother did not vary whether siblings were present or not (Brent et al. 1997).

#### **5.2.4 Sex differences in maternal investment**

There is some recent evidence that in the wild chimpanzee mothers invest more maternal effort in a particular sex. On analysing 33 inter-birth intervals in the Tai Forest, it was found that dominant females invested about 2 more years in sons, whereas subdominant females invested about 11 months more in daughters (Boesch 1997). A dominant mother has more chance of influencing her son's social status, thereby increasing his ability to gain more mates, so she should invest more in sons. A low ranking mother, on the other hand, has little chance of influencing her son's success, so she is better off investing in daughters, who will produce a limited but more certain number of offspring (Boesch & Boesch-Achermann 2000). This tendency for mothers to invest more in one particular sex depending on their rank has not yet been found for any other chimpanzee study (Boesch & Boesch-Achermann 2000).

### **5.3 Aims of this chapter**

The aim of this chapter is to determine whether injured adult female chimpanzees of the Sonso community are able to care for their dependants in the same way as

non-injured mothers, and whether dependants of injured mothers have the same social opportunities as dependants of non-injured mothers.

More specifically this chapter will determine:

- whether the proximity of the mother and dependant is affected by the injury of the mother.
- whether injured mothers carry their dependants as often as non-injured mothers, and if they have more difficulty carrying them in either arboreal or terrestrial space.
- whether mothers of very young infants, at a stage where they are completely dependent on the mother, are able to carry their dependants to the same degree as non-injured mothers.
- whether the social behaviour of the dependant, including play behaviour and time spent with other community members, is affected by the injury of the mother (grooming is analysed and discussed in Chapter 6).

## **5.4 Methods**

### **5.4.1 Definition of terms**

Dependant: in the following analyses dependant refers to the youngest dependant of the mother. Dependant is divided into four age categories: Baby, Infant 1, Infant 2 and Juvenile 1 (see Table 3.4 for definitions of Infant 1, Infant 2 and Juvenile 1).

Baby: This category refers to the two youngest infants: Janet and Katia, both were less than 12 months of age at the beginning of the study period. Definitions given in Table 3.4 place them in Infant 1, but for the purpose of this chapter they are given their own category.

Older juvenile sibling: The age category Juvenile 2 are all older juvenile siblings of dependants, and are included in one analysis only.

Table 5.1 shows the age categories and approximate date of birth of all the dependants and older juvenile siblings of the 12 study females.

**Table 5.1**      Age category and approximate date of birth (DOB) of dependants and older juvenile siblings

<i>Mother</i>	<i>Dependant</i>	<i>Age category</i>	<i>Approx. DOB</i>	<i>Older juvenile siblings</i>	<i>Age category</i>	<i>Approx. DOB</i>
Janie	Janet	Baby (Infant 1)	09 / 99			
Kewayya	Katia	Baby (Infant 1)	12 / 98			
Kutu	Kana	Infant 1	10 / 98	Kato	Juvenile 2	09 / 93
Kigere	Keti	Infant 1	09 / 98			
Ruhara	Rose	Infant 2	11 / 97			
Ruda	Rachel	Infant 2	06 / 97	Bob	Juvenile 2	91 ?
Zimba	Zig	Infant 2	06 / 97	Gonza	Juvenile 2	92 ?
Banura	Betty	Infant 2	10 / 96	Shida	Juvenile 2	92 ?
Nambi	Nora	Juvenile 1	02 / 96	Musa	Juvenile 2	93 ?
Zana	Zalu	Juvenile 1	06 / 95			
Kwera	Kwezi	Juvenile 1	01 / 95			
Kalema	Bahati	Juvenile 1	12 / 94			

N.B. The DOB of some of the older juvenile siblings is unknown (?). The years given above are estimates; although it is possible these individuals may have been born before the date given.

All of the deformities of the study females were incurred before the start of the Budongo Forest Project, in 1990 (Waller 1995). Therefore, all injuries were obtained prior to the birth of dependant subjects.



**5.4.2 Mother-dependant distance and social behaviour of the dependant**

Behaviour of the dependant, including proximity to the mother, and the dependants social behaviour, were recorded using the scan sampling method (Altmann 1974), with scans taken at five minute intervals during the half hour observation period (for more details see Chapter 3). A total of 3157 scan samples were collected on the dependants of each of the 12 mothers in the study (see Table 5.2).

**Table 5.2**      Number of five-minute scans for each mother and her dependant

<i>Focal subject</i>	<i>Dependant</i>	<i>Number of scans</i>
Banura	Betty	231
Kewayya	Katia	308
Kigere	Keti	252
Kalema	Bahati	287
Zana	Zalu	273
<i>Injured - total</i>		1351
Janie	Janet	266
Kutu	Kana	217
Kwera	Kwezi	315
Nambi	Nora	266
Ruda	Rachel	238
Ruhara	Rose	203
Zimba	Zig	301
<i>Non-injured total</i>		1806
Total		3157

Mother-dependant distance: was recorded every five minutes by using the following categories:

- 1 - dependant within one metre of the mother, including infant being carried
- 5 - dependant between one and five metres of the mother

- 10 - dependant between five and ten metres of the mother
- B - dependant beyond 10 metres from the mother
- OS - dependant and/or mother out of sight from observer

In order to determine whether the distance that a dependant spent away from its mother is affected by the injury of the mother, the data were summarized by calculating percentages of scans for each dependant at each different measure of distance. A binomial GLM was then used for analysis (see below), which included three factors: injury status of the mother, the age of the dependant, and the season. Each distance was analysed separately.

Social behaviour: the social behaviour of the dependant was recorded every five minutes. These behaviours included:

- BG - being groomed (and ID of groomer)
- GR - grooming (and ID of groomee)
- MG - mutual grooming (ID of partner)
- OM - resting on mother, includes time spent suckling
- Wi - resting within one metre of an individual in the community (not mother)
- PA, PC, PT - playing alone, playing chase (rough play), playing tickle (gentle play)
- Oth - other (including all other behaviours such as feeding, moving)
- OS – behaviour of dependant is out of sight

In order to determine whether the social behaviour of the dependant is affected by the injury of the mother, the data were summarized, by calculating percentages of scans for each dependant for each different behaviour. A binomial GLM was then used for analysis (see below), which included two factors: injury status of the mother and the age of the dependant. Social behaviours were divided into three sections and analysed separately.

### **5.4.3 Mother carrying dependant during locomotion**

Focal animal sampling (Altmann 1974) was used to determine the amount of time a mother spent carrying her dependant (for more details see Chapter 3). Whenever a mother was recorded to be moving it was also recorded whether or not she was carrying her dependant. This was recorded when moving both on and off the ground. If a mother was recorded as not carrying her dependant, the dependant was travelling without assistance from its mother or from any other chimpanzee in the group. Percentages were calculated for the amount of time the mother carried the dependant out of the total time the mother spent in locomotion, and linear mixed models were used for analysis.

### **5.4.4 Analysis methods**

All statistical analysis follows the methods described in Chapter Three. Scan data are analysed using binomial GLMs and focal animal sampling data are analysed using a linear mixed model. All analyses in this chapter use the additional age category - baby (see above for definition). The category baby was included as in many cases these infants are too young to engage in the behaviours being analysed. The age of the dependant is particularly important in these analyses owing to behavioural changes during development described above. No dependant changed age category during the study period, so any effects owing to the change in age of the dependant during the eight months of this study are not determined in these results. Season is also included as a factor in some of the binomial GLMs. The sex of the dependant would be an interesting factor that may impact on the behaviours seen; however, the sample size in the present study is too small for proper analysis. Dominance rank of the mother may be yet another factor that may affect results, since dominance rank has been shown to affect maternal investment (see 5.2.4), but accurate rankings are not available for adult females in this study (see Appendix 2).

The Bonferroni correction method (see Chapter 3) was used for data on mother-dependant distance and dependant social behaviour. The resulting significance levels were 0.0125 and 0.017 respectively. Only one test was conducted for the



data relating to the time a mother carries her dependant during locomotion, so the significance level remained at 0.05 for this analysis.

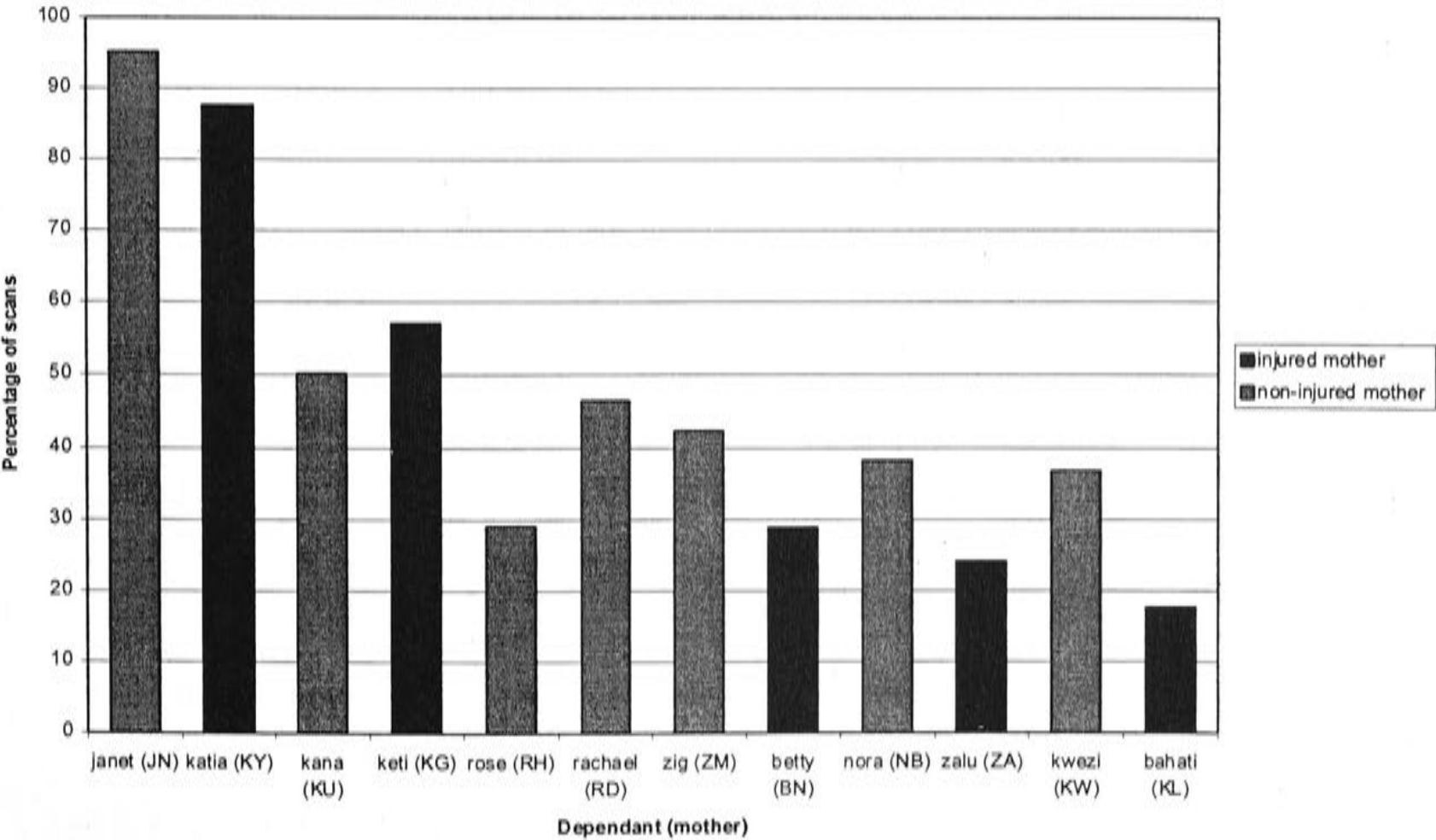
5.5 Results

5.5.1 Mother – dependant distances

Dependant within one metre of the mother

As the age of a dependant increases, the amount of time spent within one metre of their mother decreases (see Figure 5.1). All figures in this section have the youngest infant appearing on the left side of the graph, and are ordered by age with the oldest juvenile on the right. An estimate of the amount of time compared in Figure 5.1 would be 21 hours within one metre of her mother for Janet, and four hours for Bahati (out of an average total time of 22 hours). It seems possible from Figure 5.1 that the injury of the mother may have some impact on the amount of

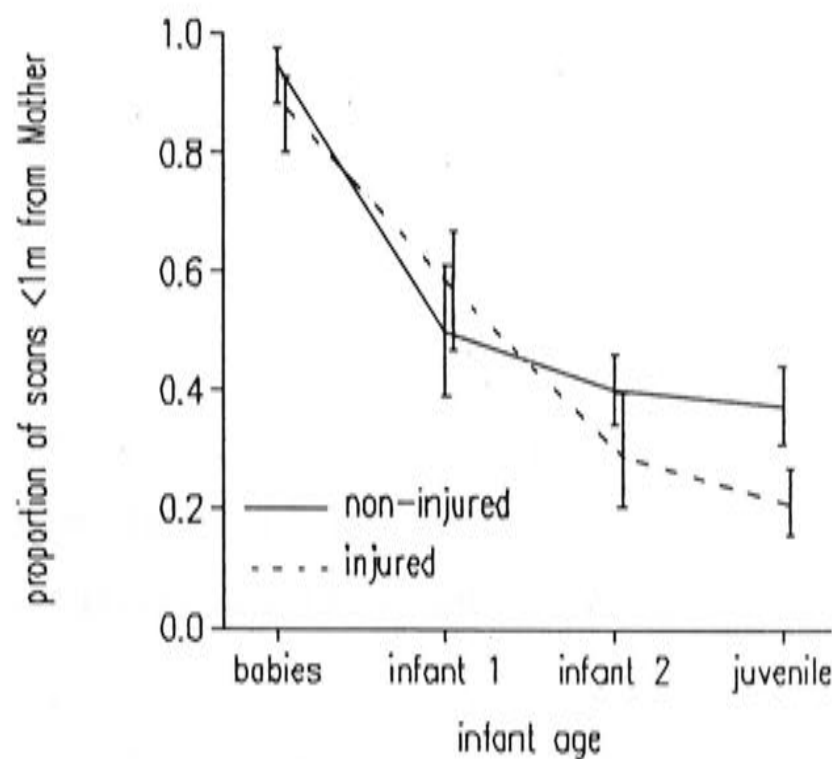
**Figure 5.1** Percent of five-minute scans that dependant was within one metre of the mother  
(refer to Table 5.2 for number of scans used in analysis)



time a dependant spent within one metre of her. Older dependants with injured mothers seem to spend less time within one metre of their mother, than older dependants with non-injured mothers. There appears to be no difference for younger dependants.

A binomial GLM was used in order to test whether dependants of injured mothers spent less time within one metre of their mothers, when compared to dependants of non-injured mothers. A significant association was found between the proportion of scans that an individual spent within one metre of the mother and both the dependant's age and injury status of the mother. As dependant age increased, the proportion of scans spent within one metre of the mother decreased significantly for all individuals ( $F=87.67$ ,  $d.f.=3,444$ ,  $p<0.001$ ). Juveniles with injured mothers spent a significantly lower proportion of scans within one metre of their mother than juveniles with non-injured mothers ( $F=13.16$ ,  $d.f.=1,444$ ,  $p<0.001$ ). Figure 5.2 shows this result. Figure 5.2 also shows that injured and non-injured mothers with babies (infants younger than 12 months) show the least difference for time in close proximity.

**Figure 5.2** Proportion of scans that each age category spent within one metre of their mother  
(refer to Table 5.2 for number of scans used in analysis)

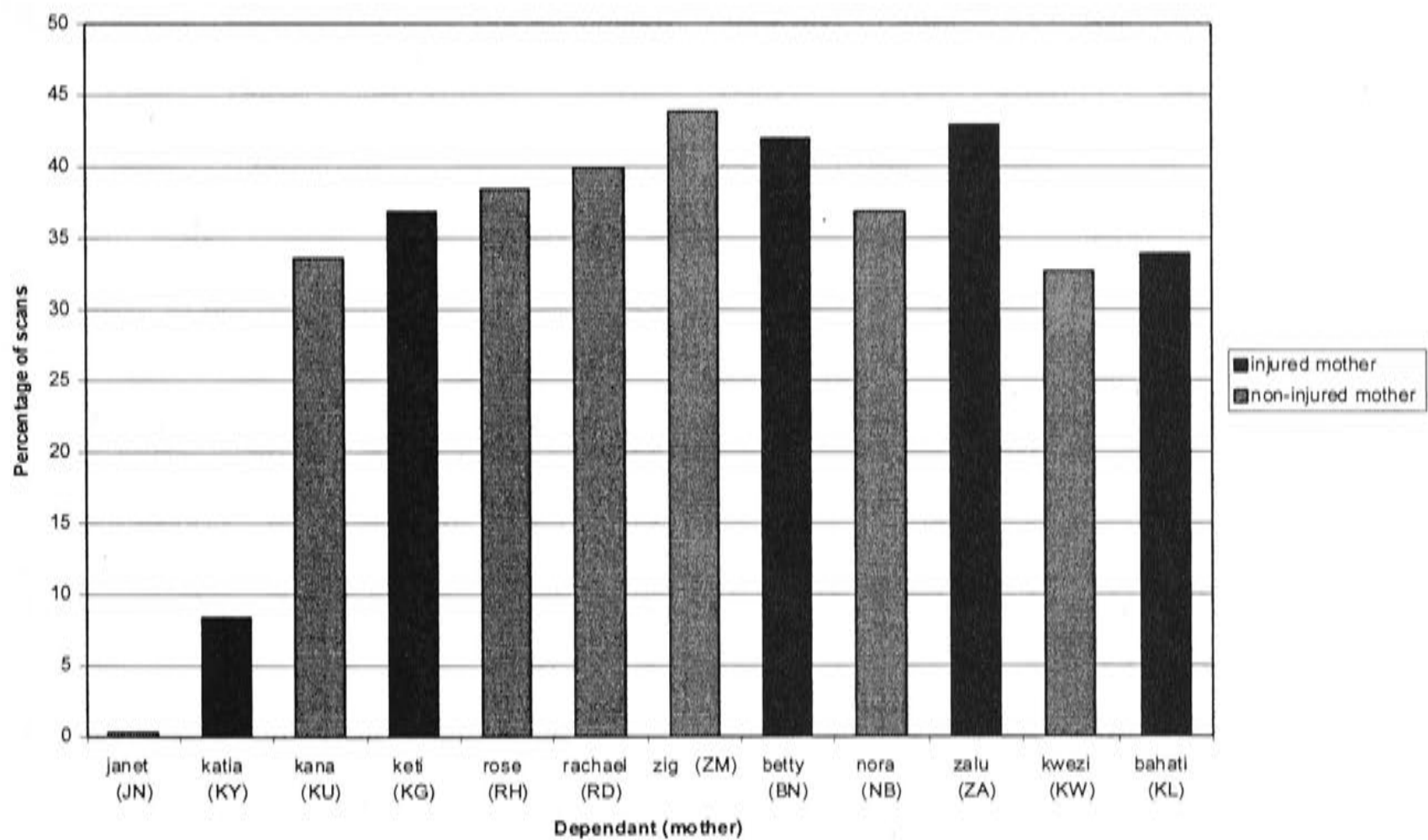




Dependant between one and five metres of the mother

Figure 5.3 shows that aside from the two youngest individuals the remainder of the dependants spent a similar proportion of scans between one and five metres from their mother. No difference was apparent for dependants of injured and non-injured mothers.

**Figure 5.3** Percent of five-minute scans that dependant was between one and five metres of the mother  
(refer to Table 5.2 for number of scans used in analysis)



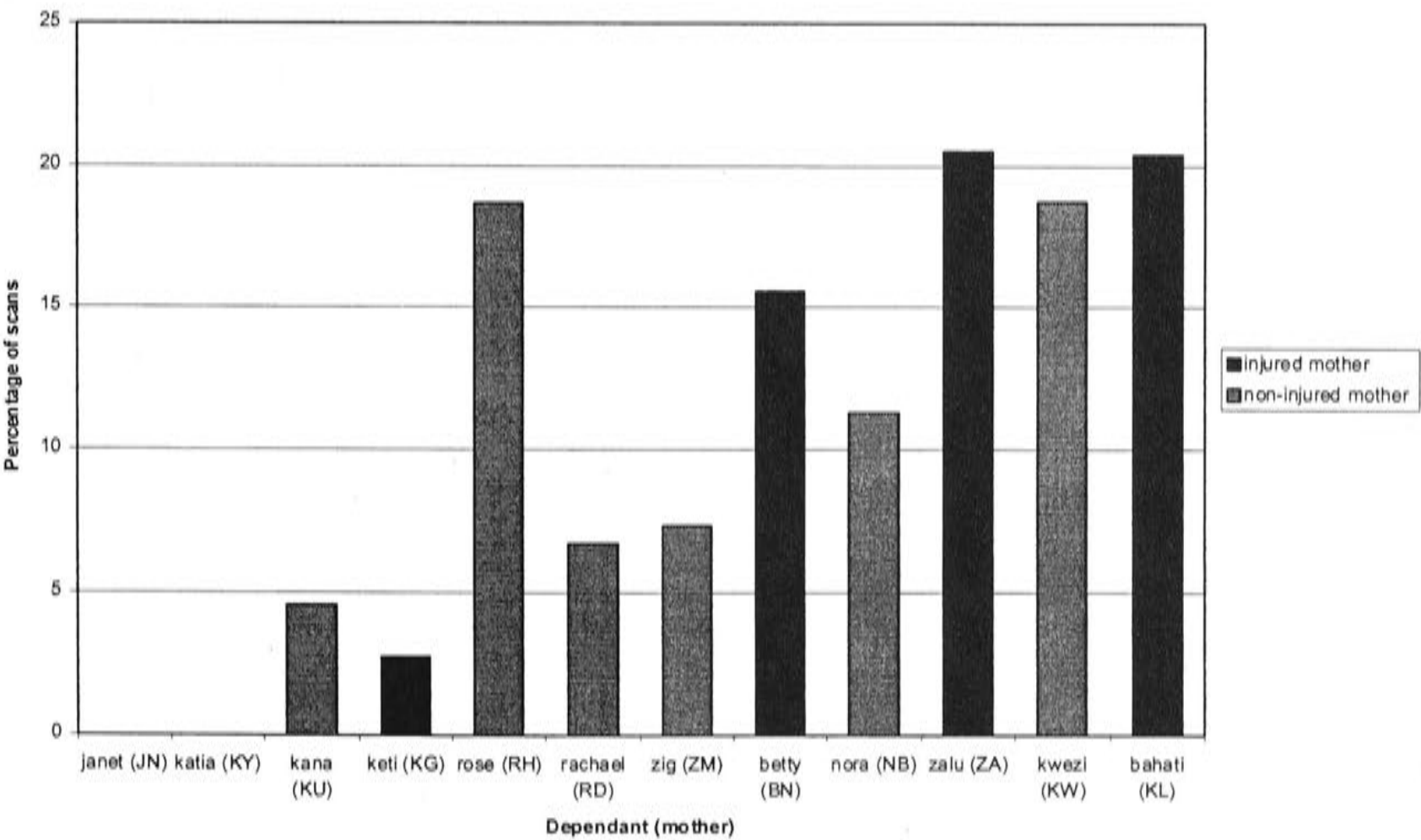
A binomial GLM revealed a significant association between the proportion of scans that an individual spent between one and five metres from the mother with both dependant age ( $F=47.97$ ,  $d.f.=3,440$ ,  $p<0.001$ ) and season ( $F=13.78$ ,  $d.f.=1,440$ ,  $p<0.001$ ). This was due to the Infant 1 dependants (Kana and Ketu), who spent a significantly higher proportion of scans between one and five metres from the mother in the wet season compared to the dry season. No significant difference was found between injured and non-injured mothers.



Dependant between five and ten metres of the mother

Figure 5.4 shows that there is a general increase in the percentage of scans spent between five and ten metres from the mother as age of the dependant increases. Also as the age of the dependant increases there appears to be an effect of the mother’s injury status: older dependants with injured mothers seem to spend a greater percentage of scans between 5 and 10 metres from the mother than those with non-injured mothers. This seems to correspond with the earlier result that juveniles with injured mothers spent less time within one metre of their mother.

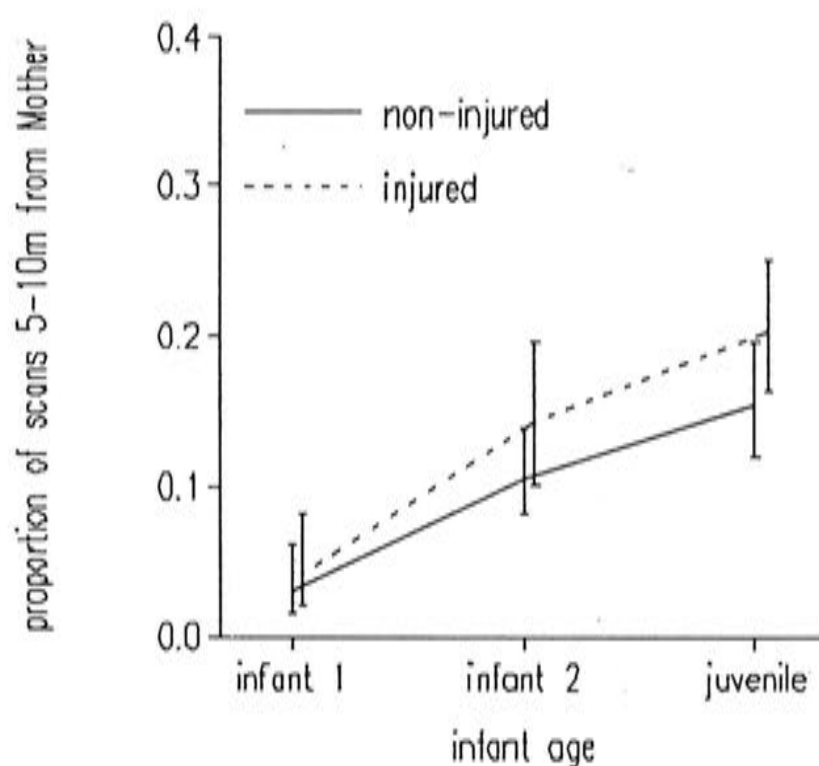
**Figure 5.4**     Percent of five-minute scans that dependant was between five and ten metres from the mother  
(refer to Table 5.2 for number of scans used in analysis)



A binomial GLM revealed that there was a significant association between the proportions of scans a dependant spent between 5 and 10 metres from the mother and dependant age ( $F=17.83$ ,  $d.f.=2,366$ ,  $p<0.001$ ); there was also a non-significant trend found for injury status of the mother ( $F=3.67$ ,  $d.f.=1,366$ ,  $p=0.058$ ). As age of the dependant increased so did the proportion of scans spent at 5 to 10 metres from the mother, as well as the effect of the mother’s injury on

the results (see Figure 5.5). Juveniles with injured mothers spent a greater proportion of scans between 5 and 10 metres than juveniles with non-injured mothers, but this result was not significant. The two youngest were excluded from this analysis, as they never ventured more than 5 metres beyond their mother (see Figure 5.4).

**Figure 5.5** Proportion of scans that each age category spent between five and ten metres from their mother



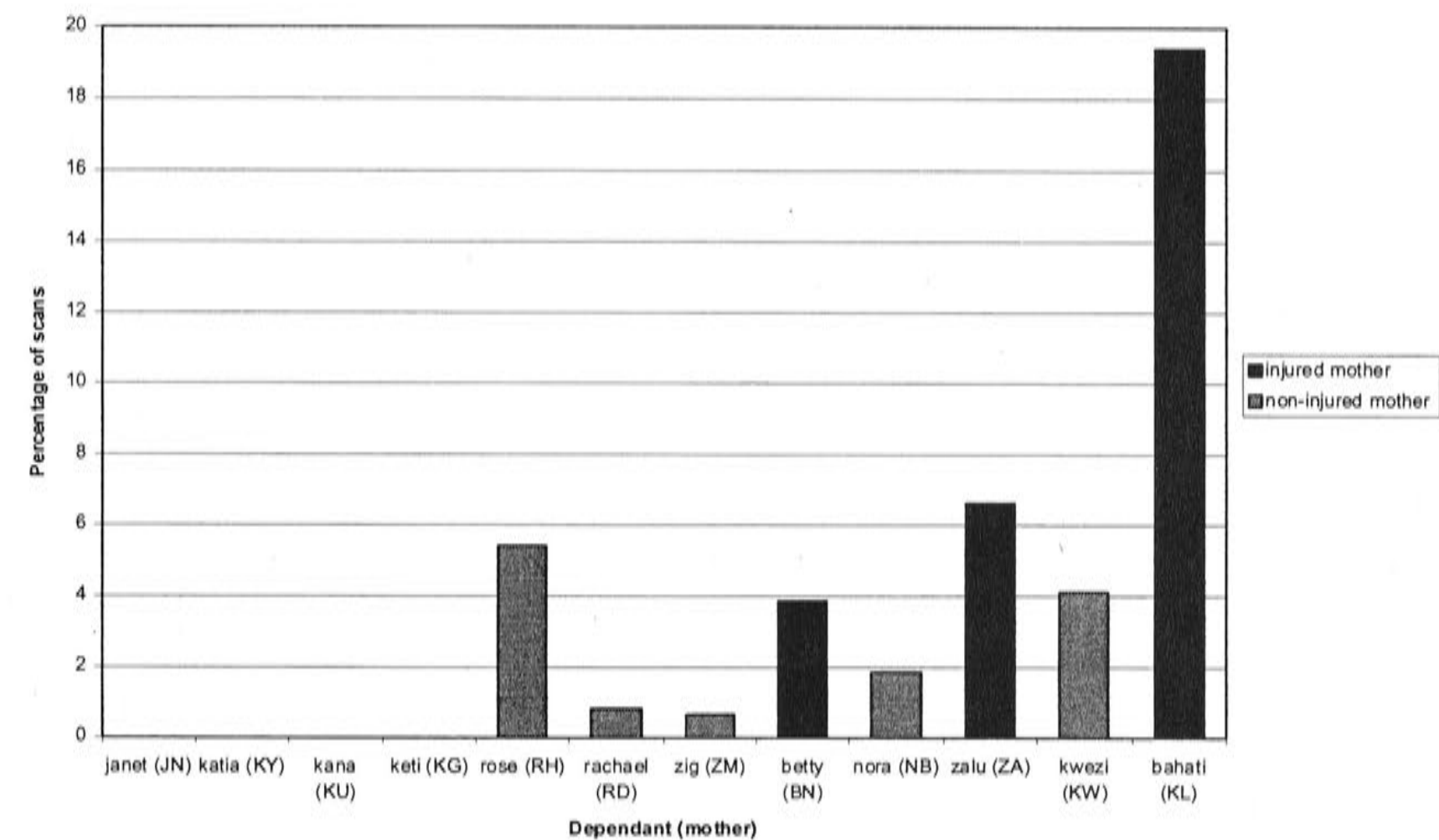
### Dependant beyond 10 metres from the mother

Figure 5.6 shows that generally the time spent at a distance beyond 10 metres increased with the age of the dependant, but only one individual (Bahati) spent greater than 7% of scans at a distance beyond 10 metres from the mother. It also appears that individuals with injured mothers spent a larger percentage of scans at this distance than individuals with non-injured mothers.

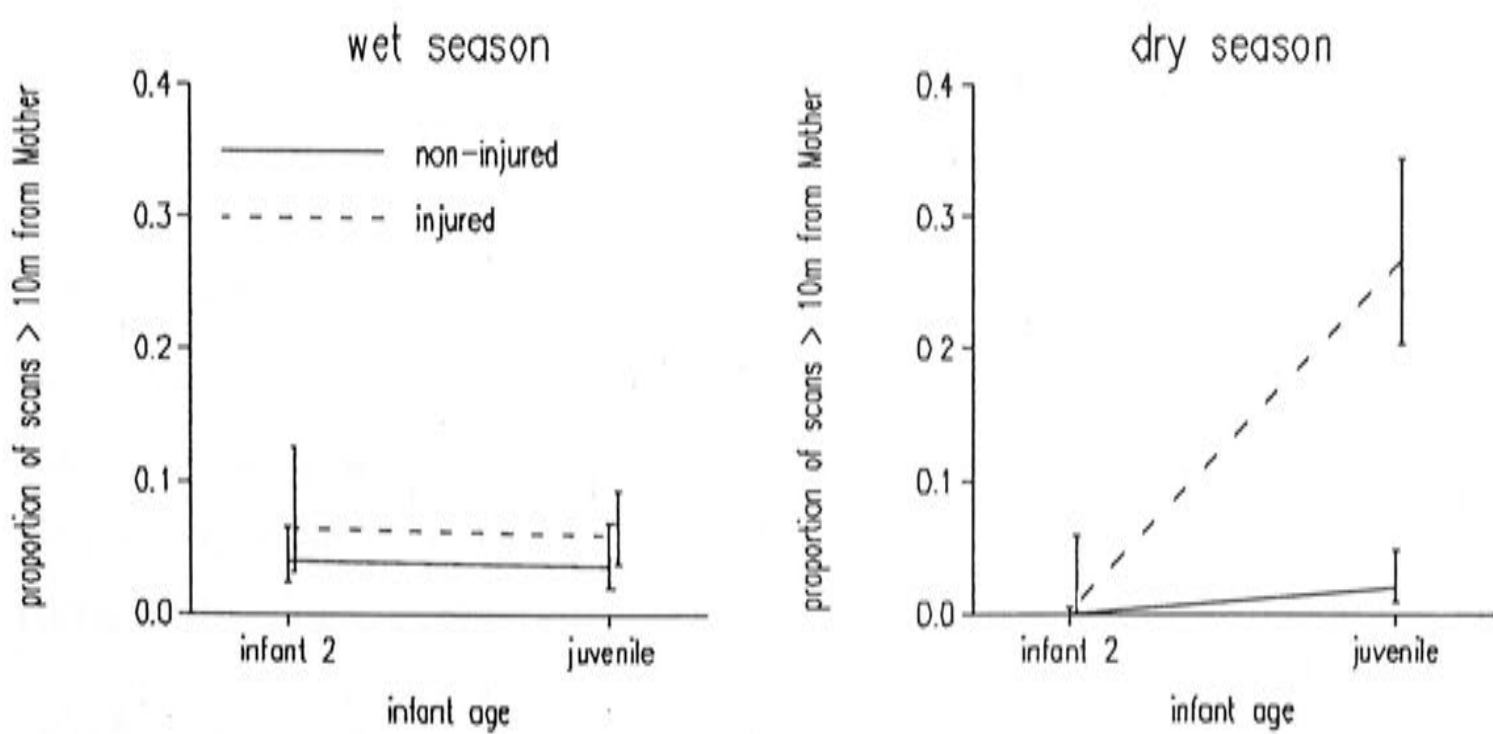
A binomial GLM revealed a significant association between the combined effect of injury and season ( $F=28.15$ , d.f.=1,297,  $p<0.001$ ), as well as dependant age and season ( $F=27.89$ , d.f.1,297,  $p<0.001$ ). The four youngest were excluded from this analysis, as they never ventured beyond 10 metres from their mother. A significant difference was found, but only for the dry season: juveniles with injured mothers spent a significantly larger proportion of scans beyond 10 metres

from the mother than juveniles with non-injured mothers, and juveniles spent a significantly larger proportion of scans beyond 10 metres from their mother than infants (see Figure 5.7). Data on season covers the eight months of the study

**Figure 5.6**     Percent of five-minute scans that dependant is beyond ten metres from the mother  
(refer to Table 5.2 for number of scans used in analysis)



**Figure 5.7**     Proportion of scans that each age category spent beyond ten metres from their mother in different seasons





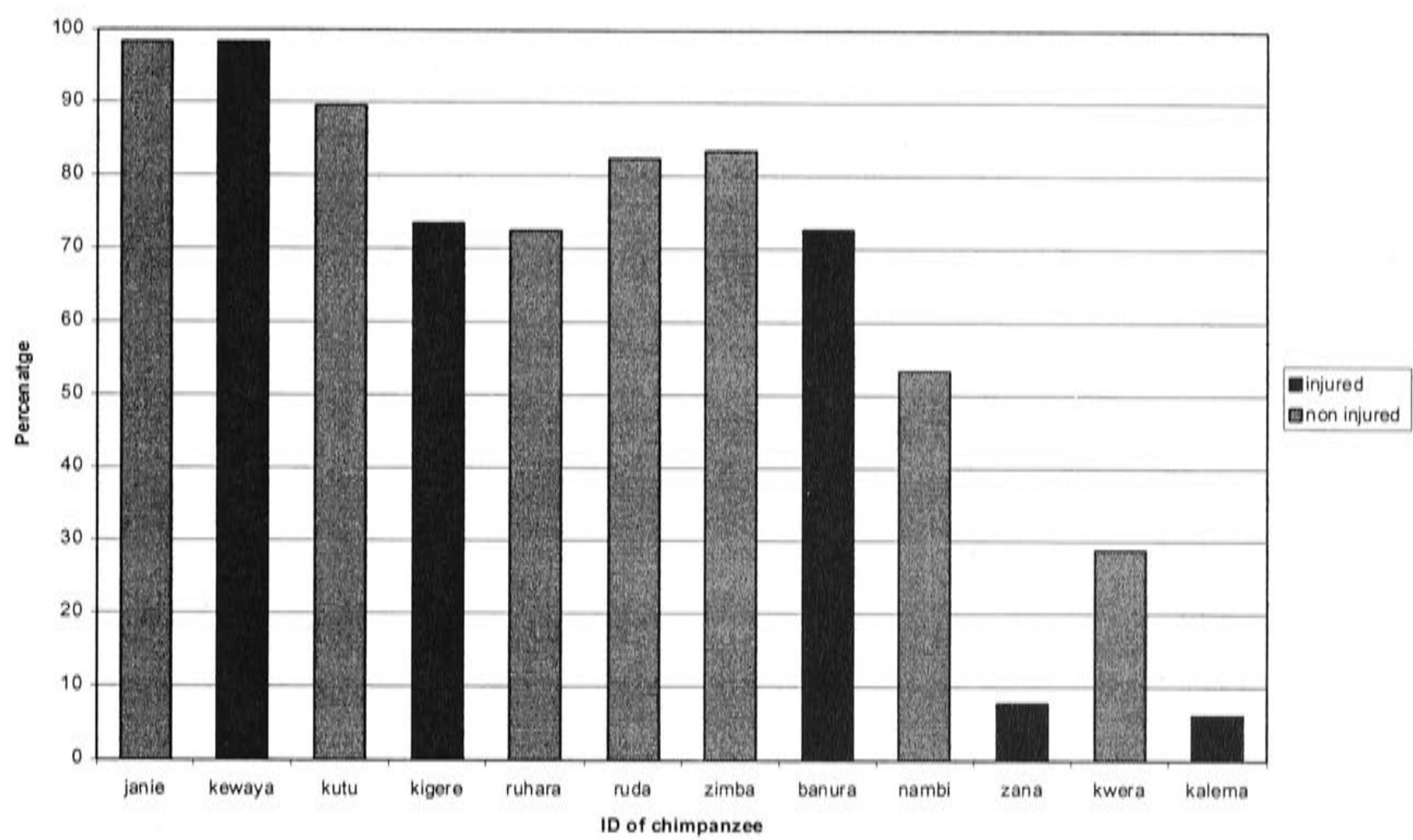
period, so analysis of season does not span an entire year. Number of observation periods, and number of months studied in each season are outlined in sections 3.4.5 and 3.4.6.

### **5.5.2 Mother carrying dependant during locomotion**

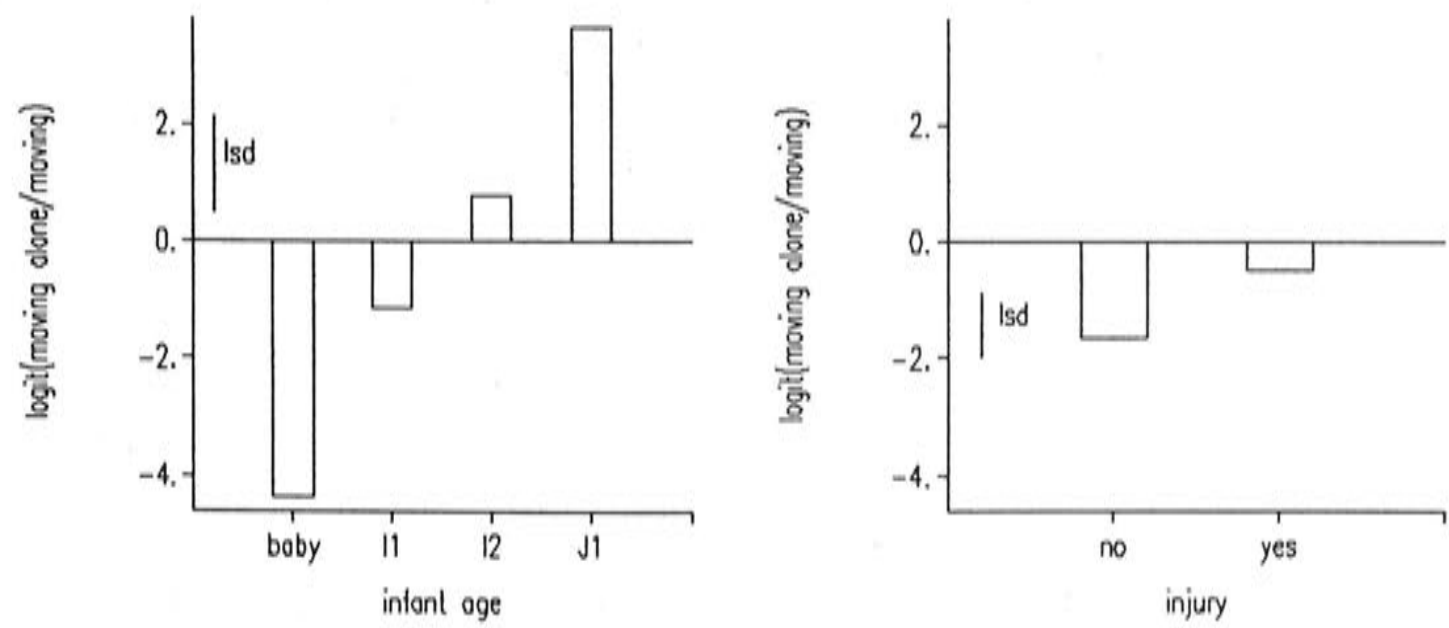
Figure 5.8 shows a general decrease in the time a mother carries her dependant as the age of the dependant increased (as with other graphs the mothers are ordered by age of dependant with the youngest dependant on the left hand side of the graph and the oldest on the right). Two of the mothers (Janie and Kewayaya) carried their infants (babies) for almost 100% of their time during locomotion; these two mothers have the youngest offspring in the community. The mothers with Infant 1 and Infant 2, shown in the centre of the graph (Kutu through to Banura), show a small difference between injured and non-injured mothers, with injured mothers carrying their offspring for less time than non-injured mothers (with the exception of Ruhara). The four mothers with juvenile offspring (on the right of the graph) show a marked difference between the amounts of time that mothers spent carrying them, the injured mothers carrying their dependants for less time than the non-injured mothers. It appears that the affect of injury on the time a mother carries her dependant is more evident as the offspring gets older.

The linear mixed model revealed that both the age of the dependant (Wald Statistic = 40.43, d.f.=2,  $p<0.001$ ) and the injury status of the mother (Wald Statistic = 4.37, d.f.=1,  $p<0.05$ ) significantly affected the time a mother spent moving without carrying her dependant. The time the mother spent moving without carrying her dependant increased significantly with the age of the offspring. Injured mothers spent significantly more time moving without carrying their dependant than non-injured mothers. These results are shown in Figure 5.9. Babies were found to be significantly different from other age classes (Wald Statistic = 66.90, d.f.=1,  $p<0.001$ ) with respect to the time they were carried by the mother, and from Figure 5.8 it can be seen that babies were carried for almost 100% of the time a mother was travelling.

**Figure 5.8** Time mother spent carrying dependant as a percentage of total time in locomotion  
(refer to Table 3.6 for number of observation periods and total time observed)



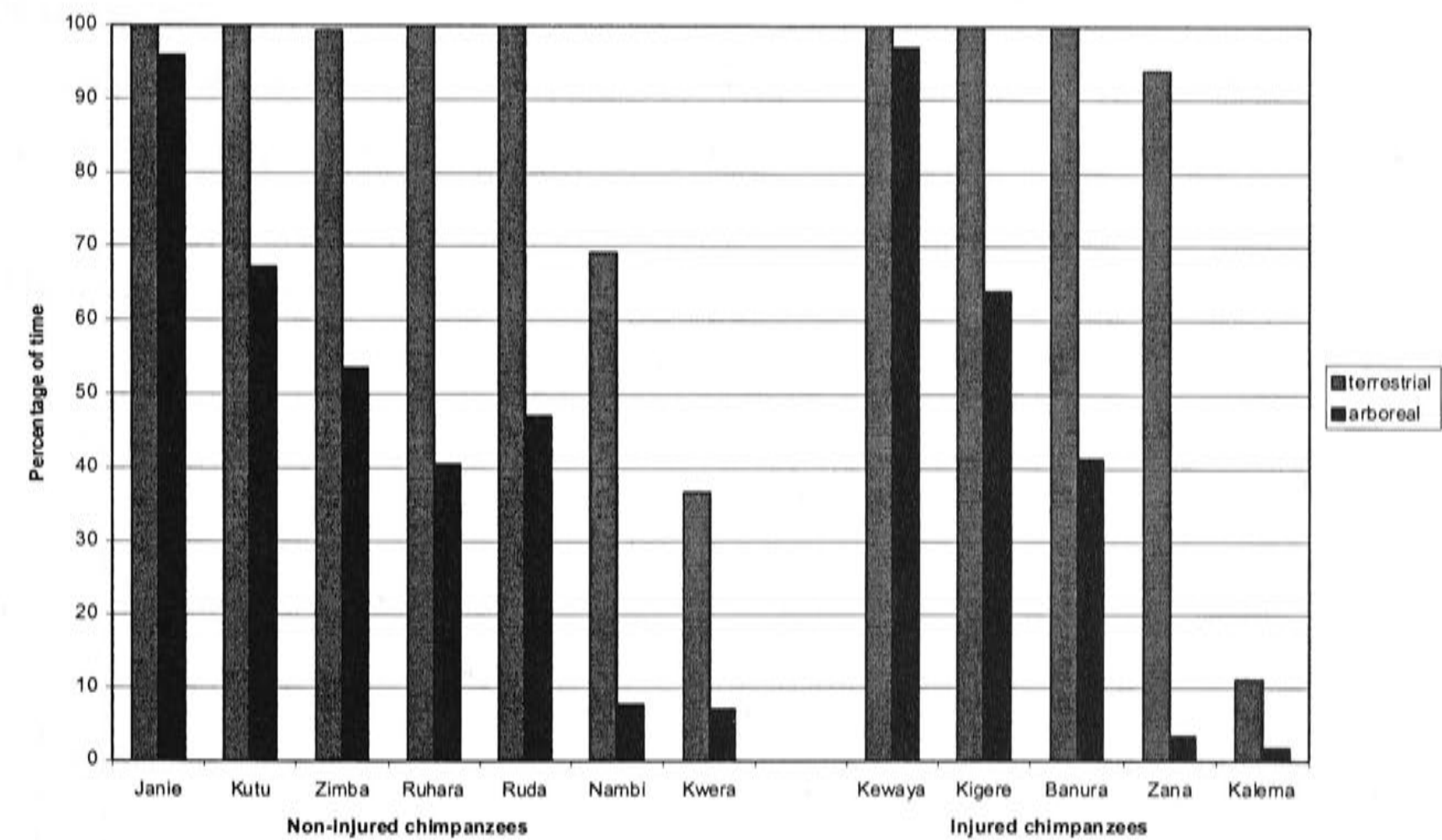
**Figure 5.9** Time mother travelling without carrying dependant for different age classes and injury status



Injured mothers may have more difficulty carrying their dependants, depending on whether they are travelling on the ground or in the trees. Figure 5.10 shows the

percentage of time a mother carried her dependant, out of the total time she was moving, in both arboreal and terrestrial space. As the age of the dependant increased, the amount of time the mother spent carrying it decreased. The age at which an infant began travelling alone was different in arboreal and terrestrial space. Mothers continued to carry infants and juveniles in terrestrial space for far longer than in arboreal space; even Infant 1 moved on their own in the trees. This may be because long distances are most commonly travelled on the ground. There appears to be no difference between injured and non-injured mothers.

**Figure 5.10** Percentage of time that mother carried dependant in terrestrial and arboreal space  
(refer to Table 3.6 for number of observation periods and total time observed)



### 5.5.3 Social behaviour

#### Social play behaviour

Figure 5.11 shows that the percentage of scans spent playing was greater for younger dependants with injured mothers than older dependants with injured

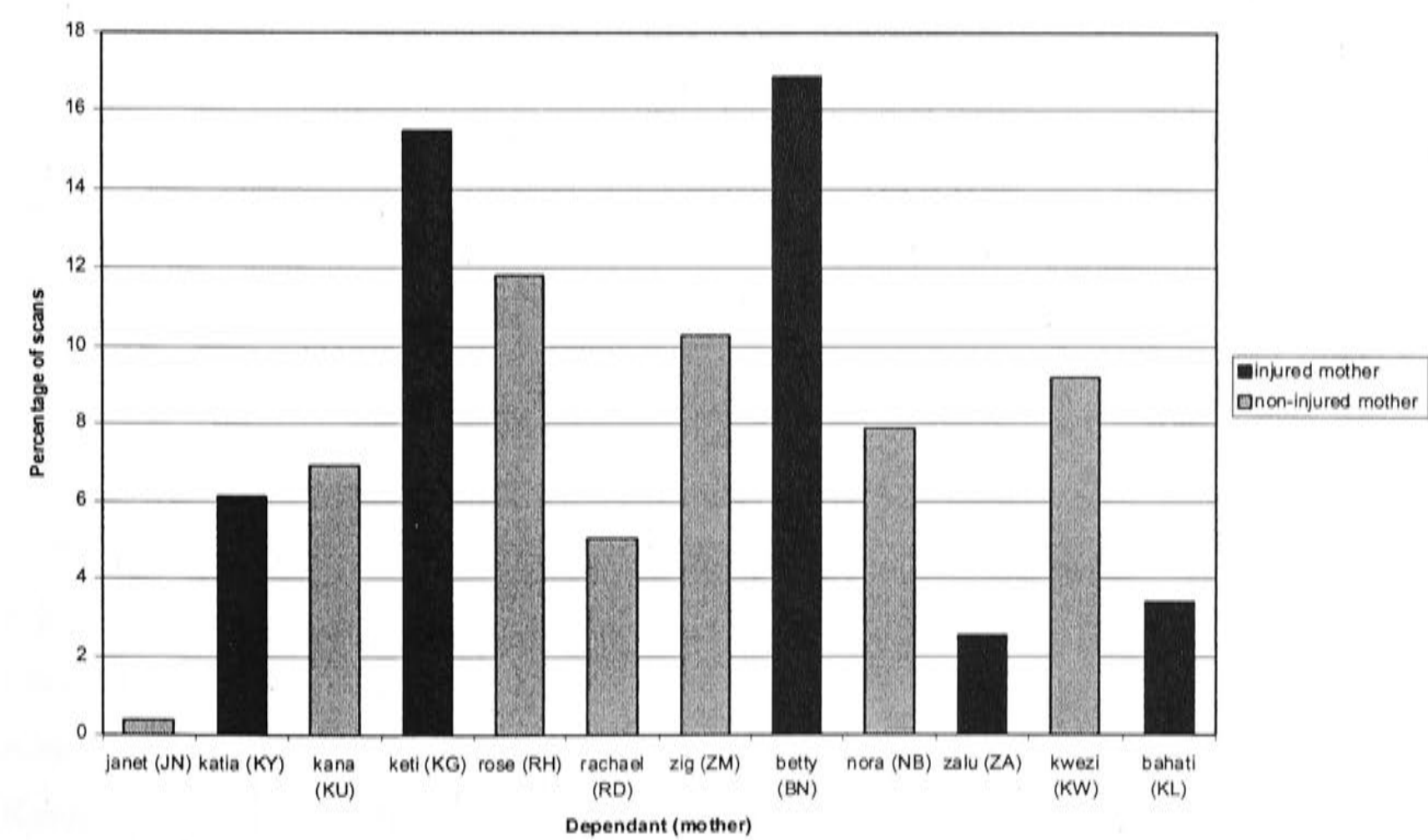


mothers, whereas there was no corresponding difference in time spent playing for dependants of non-injured mothers. Juveniles with injured mothers played less than juveniles with non-injured mothers, and infants with injured mothers played more than infants with non-injured mothers, with the exception of the two youngest (babies).

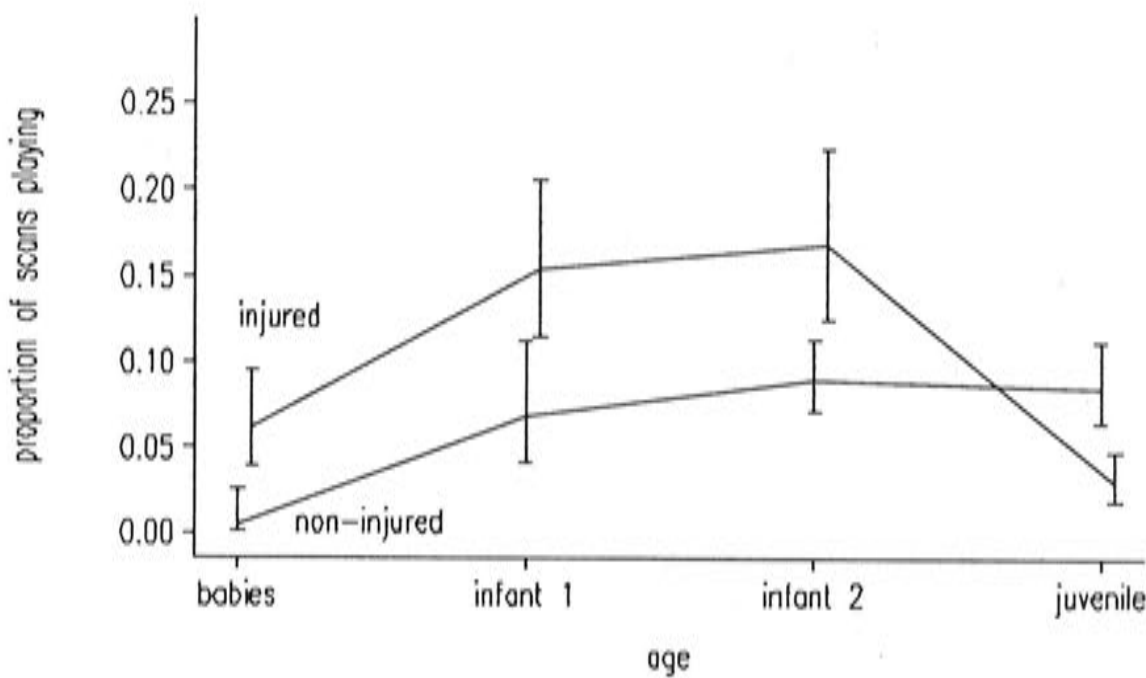
A binomial GLM revealed that there was a significant association between the amount of time playing and the combined effect of injury status of the mother and age of the dependant ( $F=16.26$ ,  $d.f.=3, 444$ ,  $p<0.001$ ). Both Infant 1 and Infant 2 with injured mothers spent significantly more time playing than infants with non-injured mothers; and juveniles with injured mothers spent significantly less time playing than juveniles with non-injured mothers (see Figure 5.12).

N.B. The result for babies is influenced by the inclusion of Janet (who had a non-injured mother); she was too young to play with other individuals, and was only recorded playing with her mother at one scan.

**Figure 5.11** Percentage of five-minute scans where dependant is playing (refer to Table 5.2 for number of scans used in analysis)



**Figure 5.12** Proportion of scans spent playing for each age category



As a measure of sociability it is important to see whether dependants are playing only with closely related individuals (i.e. their mother or older siblings) who are easily available to them, or if they spend their time playing with other community members, which means they are getting more opportunities for social interactions. Table 5.3 shows that for all dependants the majority of time spent playing was

**Table 5.3** Number of scans where dependant was playing with different age categories (dependants with injured mothers are in **bold**)

Dependant	Number of scans dependant was playing with each age category			
	Mother	Sibling	Infant/Juvenile	Other
<b>Bahati</b>	0	-	10	0
<b>Zalu</b>	0	-	7	0
<b>Betty</b>	0	1	34	2
<b>Keti</b>	5	-	32	0
<b>Katia</b>	6	-	13	0
Kwezi	0	-	23	3
Nora	1	5	14	1
Zig	2	3	25	0
Rachael	0	3	10	0
Rose	0	-	21	3
Kana	0	7	9	0
Janet	1	-	0	0

with unrelated infants and juveniles. Janet, the youngest member of the Sonso community, was too young to play with others (as mentioned above).

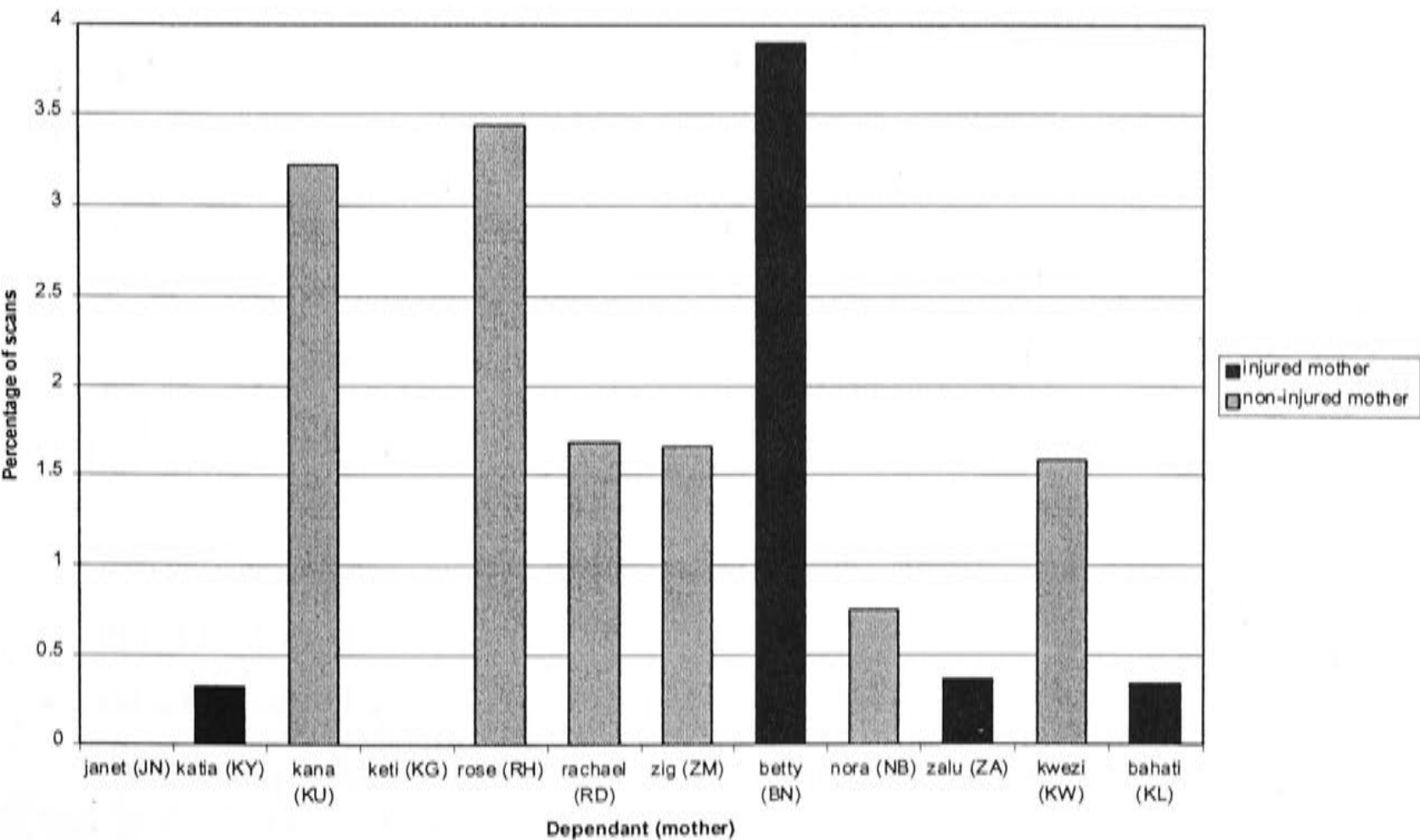
Grooming behaviour

The grooming behaviour between the mother and her dependants is analysed and discussed in Chapter Six.

Interactions with individuals other than the mother

Figure 5.13 shows the percentage of scans where a dependant was within one metre of another individual in the community other than their mother. There seems no pattern according to either age of dependants or injury status of the mother. Other individuals include siblings, so the presence of siblings may influence these results. Kana, Betty and Rachael all have juvenile siblings (2 siblings are male and 1 is female); the majority of scans shown in Figure 5.13

**Figure 5.13** Percent of scans dependant was within one metre of an individual other than its mother  
(refer to Table 5.2 for number of scans used in analysis)





were from when they were within one metre of them. On the other hand Nora and Zig, who also have juvenile siblings (1 sibling is male and 1 is female), were never observed within one metre of them at scans. One infant with no siblings (Rose) had the second highest percent of scans within one metre of another individual. The presence of siblings, or the sex of the siblings present, does not seem to affect these results.

A binomial GLM revealed a significant association between the proportion of scans where a dependant was observed within one metre of an individual other than their mother and the combined affect of age of the dependant and injury status of the mother ( $F=5.36$ ,  $d.f.=3,444$ ,  $p=0.001$ ). The effect seen was due entirely to the age category Infant 1, and so it is likely that individual difference alone accounts for the result, rather than age or injury status.

#### **5.5.4 Summary of Results**

- Juveniles with injured mothers spent significantly less time within one metre of their mother than juveniles with non-injured mothers.
- Juveniles with injured mothers spent significantly more time beyond 10 metres from their mother than juveniles with non-injured mothers, but only in the dry season.
- Mothers with injuries are in close proximity to their very young infants (babies) to the same degree as mothers without injuries. Injured and non-injured mothers carried babies for almost 100% of their travelling time.
- Injured mothers were significantly less likely to carry their dependants while moving than non-injured mothers. No difference, with respect to injury, was found for moving in either in arboreal or terrestrial space.
- Age of the dependant affected both the proximity of the mother and dependant (close proximity decreased as age increased) and the likelihood of the mother carrying the dependant (less likely as age increased).
- Infants (not including babies) with injured mothers spent significantly more time playing than infants with non-injured mothers; and juveniles

with injured mothers spent significantly less time playing than juveniles with non-injured mothers

## **5.6 Discussion**

### **5.6.1 Mother - dependant distances**

As would be expected from the literature review (Assersohm 1999; Silk & Kraemer 1976) younger infants in this study spent significantly more time in close proximity to their mothers, and gradually, as they got older, they spent more time at distances further from them.

During the early stages of an infant's development, when infants are completely dependent on the mother, injured mothers of the Sonso community were seen to be in close proximity (within one metre) of their dependants (babies) as often as non-injured mothers. It is crucial to a young infant's survival that it be completely supported by its mother. It seems that the differences become apparent only as the dependants become older, and either have more of an opportunity for independent living, or are able to fend for themselves with less of a risk to their survival.

The effect that the mother's injury had on the distance between the mother and the dependant was greatest for juveniles. For distances greater than 5 metres there was a trend seen for juveniles with injured mothers who spent more time away from their mother than juveniles with non-injured mothers; for distances greater than 10 metres this difference was significant. They also spent significantly less time within one metre of their mother.

These results show that as dependants get older, the injury status of their mother has more of an impact on their behaviour. Perhaps juveniles have more need to be independent from their mother, if their mother is injured, and thus spend more time at distances further from her. Perhaps injured mothers spend less time moving, and so as their dependants grow older, and have the confidence to travel at distances from their mother, they travel further from their mother. The two most



severely injured mothers did move less than the other mothers in this study (see Chapter 7), but only one of these had a juvenile.

Another factor that influences the results is season; juveniles with injured mothers spent a significantly greater proportion of scans beyond 10 metres in the dry season. A corresponding difference was not found in the wet season. As food sources appeared more difficult to find in the dry season (see section 3.4.6), all mothers travelled significantly more (see Chapter 7), so perhaps this influenced juveniles with injured mothers to travel distances further from their mother in search of food during the dry season. It must be noted that data were not collected for an entire year, and so season refers only to the wet and dry months of the study period.

Injured mothers were seen to carry their dependants less than non-injured mothers (for further discussion see below). It is possible that because juveniles were carried less, they spent more time at a distance from their mother, although other age-classes were also carried less, and a corresponding difference in proximity was not found.

### **5.6.2 Mother carrying dependant during locomotion**

Injured mothers were found to carry their dependants less than non-injured mothers. Injured mothers may find it more difficult to carry a dependant owing to their modified and sometimes more cumbersome locomotion (see Chapter 7). They do have difficulties when trying to move through difficult substrates, such as when travelling from the extremities of one tree to another, or when climbing and scrambling through tangled vegetation. Injured mothers may also carry dependants less because of the extra weight involved in carrying. As the weight of the offspring increases the effort imposed on the mother to carry must also increase. Furthermore, older dependants move around on the mother during locomotion – changing from ventral carrying to dorsal, or reaching out to grab at passing by objects, or by jumping on and off as the mother moves, creating a potentially unbalanced weight.



It would seem that as dependants get older and heavier, injured mothers are more likely to travel without them, and even refuse to carry them. One of the juvenile dependants (Zalu), with an injured mother (Zana), was observed being pushed off his mother, while she was travelling (see description at beginning of this chapter). It is possible that the mother was simply weaning the juvenile, but in context with the difficulties of arboreal travel it is possible that the mother was avoiding carrying the juvenile.

The two youngest dependants (babies), both younger than 12 months, were carried for almost 100% of their mothers' travelling time (Figure 5.8). Younger infants are more dependent on their mother and usually do not travel on their own until about 2 years of age (Hiraiwa-Hasegawa 1990a). Young infants also stay in close proximity to their mother, for example Figure 5.1 shows that the two youngest infants stay within 1m of their mother for more than 85% of their time. It appears from these results that very young infants are still carried to the same extent regardless of the mother's injury, and that differences are only apparent when infants become older and are able to travel independently.

Injured mothers did not show any preference for carrying their dependants in arboreal or terrestrial space. All mothers carried their dependants until an older age when on the ground compared to when they were arboreal. This may be because there are fewer dangers in arboreal space (see Chapter 7); or may be because long distance travel is more common on the ground, and mothers are more likely to carry dependants over long distances. It may also be because dependants find it easier, or more fascinating, to clamber freely in trees, than on the ground, or because mothers find it easier to carry dependants when on the ground.

### **5.6.3 Social behaviour**

An infant's social behaviour is not adversely affected by the injury of the mother, which suggests that infants of injured mothers have around the same social opportunities as infants with non-injured mothers. In fact infants who were old enough to play, were found to play more if they had injured mothers than if they

had non-injured mothers. Hemelrijk and Kogel (1989), in a study of captive chimpanzees, found that infants with more social mothers unexpectedly played less than infants with less sociable mothers. It has been found in this study that injured females spent more time alone with their dependants, and so can be considered less sociable than non-injured mothers (see Chapter 4). Hemelrijk and Kogel (1989) suggest that the attention more sociable mothers spend on other group members may be at the expense of attention given to her infant. I do not believe this applies to the Sonso community, partly because I do not think more sociable mothers spent less time with their infants, and also because it has been found in this study that social play in infants is most common with unrelated infants and juveniles, rather than the mother. I think it is possible that infants, who get less opportunity for social play because their mother spends more time alone, use any opportunity they get for social play to the fullest. It could be also argued that infants with injured mothers play more as they spend more time away from their mother, but there is no corresponding result for the time an infant spends within one metre, or between one and five metres from their mother.

Juveniles, on the other hand, do seem to be affected by the injury status of their mother in the time spent playing: juveniles of injured mothers played for less time than juveniles of non-injured mothers. Play behaviour decreases with age in both males and females (Hayaki 1985), around the time of puberty (Goodall 1968). Juveniles with injured mothers may begin decreasing their play behaviour earlier as they may mature earlier, spending more time in other social behaviours, such as grooming. Results in Chapter 6 show that although some juveniles with injured mothers were seen to groom their mothers more, statistical analysis found no overall difference. Alternatively juveniles with injured mothers may play less, as they may need to spend more time in feeding, moving, or other activities. It is possible that they do spend more time feeding, as they use more energy, because they are carried less. Maybe juveniles are less likely than infants to spend as much time as possible playing, when they have the opportunity.

Another measure of sociability was the identity of play partners. For the majority of scans where dependants played, the partner was an unrelated infant or juvenile; related individuals (mother and siblings) were involved in play behaviour, but not



to the same extent. It was very rare for dependants to play with older, unrelated individuals. This was the same pattern for dependants of injured and non-injured mothers. Sociability was also measured by recording the time a dependant spent within one metre of another individual; levels were low for all individuals. This suggests that alloparental behaviour is also low, for both dependants of injured and non-injured mothers. If injured mothers in the study group had been unable to care for their offspring, there may have been more evidence of alloparental care. The only report of an individual taking on a caring role of an offspring of an injured mother was an anecdotal observation made by Fawcett (2000). The juvenile son, Bwoba, of an injured mother, Zana, spent more time with another mother (non-injured), Kwera (see section 2.2.5.2). The observation did not mention any handling or grooming by Kwera, so it is unknown if this occurred, or if Bwoba just spent more time with Kwera. No examples of this behaviour were seen in the present study period.

Factors that may affect the mother's sociability, and in turn affect her dependants' opportunities for social interactions, such as the rank and oestrous state of the mother (Matsumoto-Oda 1999), seem also to have had a limited affect on the overall sociability of young chimpanzees at Sonso. In a captive study it was found that maternal dominance was not associated with infants' sociability (Hemelrijk & de Kogel 1989), and in the present study ranking between the mothers was very difficult to determine (see Appendix 2). The oestrous state of the mother has very little impact on the results in this chapter as only two of the study females were in oestrus during the study period (see section 6.7.3). The presence of older siblings did not appear to affect the results in a consistent way for dependants in this study. Other studies have shown that an older sibling does not reduce the amount of time a dependant spends in social interaction; rather infants with older siblings spend more time socialising with them than with other community members (Brent et al. 1997).

#### **5.6.4 Possible short and long term implications**

Once a dependant reaches juvenile age it gradually becomes more independent of the mother. The juveniles studied in this chapter are Juvenile 1 (between four and



six years) and by definition they are moving on the ground and in the trees, and feeding independently of the mother (see Table 3.4). Other studies have also found this age to be where a young chimpanzee shows many signs of independence, for example chimpanzees walk more than they are carried at around four years of age (Hiraiwa-Hasegawa 1990a), and weaning occurs at around five years of age (Pusey 1976). These results show that it is at this stage where the effects of an injured mother are seen; juveniles of injured mothers spent more time at distances further away from the mother, and less time in close proximity to the mother. They also spent less time playing. It appears that juveniles of injured mothers are becoming more independent and more socially mature at an earlier age than juveniles of non-injured mothers. This difference is not seen for infants who are still dependant on the mother. The age at weaning, and the number of years of maternal investment, may be interesting to compare for injured and non-injured mothers, although it was not possible to determine this in the present study. If dependants of injured mothers are weaned earlier, maybe this explains the increased time spent away from the mother, as the dependant would then be responsible for finding all of their own food. Early weaning, or independence, may have long-term behavioural implications for offspring of injured mothers. The only example in the present study is that of Bwoba, the sub-adult son of Zana. He is by far the lowest ranking of the males, and is very unsocial compared to other sub-adults (personal observation). He was often the last member in a large travelling party, and had very little confidence when researchers were present (personal observation). It is possible that his behaviour is associated with the lack of social opportunities he had when he was young, although these observations are only anecdotal. Long-term studies could reveal if there was any behavioural or other change in adults and sub-adults of injured mothers that may relate to them having to be more independent at an earlier age.

Injured mothers were seen to carry their dependants less than non-injured mothers, excepting the two youngest dependants who were carried almost all of the mothers' travelling time. This result could have short and long-term implications. Mentioned earlier in this chapter are examples of where death and illness have occurred because infant chimpanzees have been the subject of inappropriate or no maternal behaviour (Pusey 1983; Rijt-Plooij & Plooij 1988). Short-term effects on

the dependant could include loss of weight from travelling alone more frequently, higher stress levels, need for extra feeding, and more time spent at distances further from the mother. Of these, only distance from the mother was recorded in this study, and only juveniles with injured mothers spent more time away from mothers. Although other factors were not recorded, informal observations did not suggest that they were occurring. It is possible that juveniles spent more time feeding, as suggested above as a reason for their reduction in play time, or because they are weaned earlier. Long-term studies once again are the only way of determining whether these factors are occurring, as well as determining the effects that a reduction in time being carried as a young chimpanzee may have on sub-adult and adulthood.

## **5.7 Conclusion**

It is shown in this chapter that once a dependant reaches an age whereby it is more independent of the mother, and able to feed and travel by itself, a mother may begin to give less support to the dependant if she herself is injured. During the very early stages of an infant's development, when an infant could not survive without its mother's support, an injured mother is just as supporting as a non-injured mother. Long-term studies are necessary to determine whether dependants of injured mothers show any behavioural differences as sub-adults and adults.

## Chapter Six

### The impact of injuries on free-living chimpanzees: grooming behaviour

*Zimba and Kewayaya (thought to be mother and adult daughter), and their two respective infants Zig and Katia were resting after a long feeding session. They were sitting on a small branch high in the canopy, both using an overhanging branch to hold onto for balance. Zimba turned away from Kewayaya, who is injured, and presented her back for grooming. Kewayaya began grooming her mother while Katia looked on. After a few minutes Zimba moved, and Kewayaya had to stop grooming and reach up to the branch overhead with her one able hand to gain balance. Her injured hand could not be used for either grooming or balance in the position she was sitting. Zimba then turned to face Kewayaya and using one hand holding the branch overhead she leant out to reach around and groom Kewayaya's back and side with her other hand. Zimba's side was in the exact position now for Kewayaya to groom mutually but Kewayaya was unable to reciprocate grooming with Zimba unless she let go of the hand that she was using for balance. After a few minutes of being groomed Kewayaya finally let go of the branch above and groomed her mother, whilst being groomed, putting her in a much less stable position. (Budongo Forest: March 2000)*

#### 6.1 Introduction

Grooming serves many functions in chimpanzee society; not only does it have the role of skin care, but it is also well recognised to serve many different social purposes (Goodall 1986; Nishida 1988; Simpson 1973). The process of grooming fulfils the role of skin care by protecting the skin against parasites; a groomer will rid the skin of ticks, lice and other ectoparasites during a grooming session. Social grooming is especially important for hygiene as the groomer can reach areas of the groomee's body that the groomee cannot reach itself when self grooming (Dunbar 1988; Hutchins & Barash 1976; Nishida 1988). Grooming also has a social role in chimpanzee society. If grooming was purely for the function of hygiene then the time spent grooming per individual should increase directly with



body mass; but Dunbar (1988) found no correlation between body size and time spent grooming, instead an increase in time spent grooming was correlated with an increase in group size. This suggests that time spent grooming has more to do with social complexity than with hygiene (Dunbar 1988). There are many examples of how grooming plays a role in the social life of chimpanzees. Allogrooming contributes to the building and reinforcing of social relationships, especially in the development of alliances in chimpanzees (Watts 2000b). Male chimpanzees use grooming to establish and maintain within-community alliances, as grooming allows individuals to gain familiarity with each other and develop trust between individuals (Dunbar 1988). A female chimpanzee tends to mate with males that have shown high frequencies of affiliation with her, such as grooming and food sharing (Nishida 1988). Grooming is frequent during times of instability (Goodall 1986) since grooming is used to calm tensions after agonistic interactions (Dunbar 1988). Grooming is even used as a form of social manipulation; an infant when being weaned will use the 'groom-while-suckle' method, grooming the mother around the nipple while slowly moving in to the nipple to suckle (Nishida 1988). Both Goodall (1986, p. 406) and de Waal (1982, p.138) give examples of adult males trying to break up grooming sessions between rivals, suggesting that chimpanzees can predict the effect of mutual grooming by others. Grooming also provides the opportunity for long sessions of relaxed and friendly physical contact, both at times of stress, but also for the simple purpose of pleasure and relaxation (Goodall 1986).

Grooming may be physically difficult or impossible for chimpanzees with injuries to the limbs. Primates that are solitary for a period of time and do not get groomed almost certainly suffer poorer health, such as an increase in the number of ticks or infestations of ectoparasites (Ghiglieri 1984). If chimpanzees with injuries show reduced levels of self or social grooming this could affect their health. As has been discussed earlier in this thesis non-injured chimpanzees may lack tolerance or acceptance of injured individuals, and so levels of grooming in a social group may be affected. Previous studies have used grooming to determine the level of friendly and affiliative relationships (Sugiyama 1988), and the level of reciprocity among individual chimpanzees (Nishida 1988), and for analysing inter-individual relationships (Simpson 1973).

This chapter begins with a discussion of grooming methods used by chimpanzees and the factors affecting the level of grooming seen. The aims of the chapter are then stated followed by an analysis and discussion of how injury may be affecting grooming in wild chimpanzees of the Sonso community.

## **6.2 Methods of grooming used by wild chimpanzees**

Chimpanzees groom socially sitting or lying close together, either on the ground or resting on a branch in a tree. The act of grooming involves the groomer running one or both hands through the hair of the groomee. Sometimes just one finger casually parts the hair, at other times grooming is more vigorous with great attention given and both hands used (Goodall 1968). The general method used involves the hair being parted so as to expose the skin in the search for ectoparasites, dry skin or foreign material. When ticks or lice are found, the groomer picks off the ectoparasite with their mouth or fingers (Goodall 1968). Successful or attentive grooming involves both hands, one to part the hair and the other to pick off whatever is found, and sometimes the mouth is used to eat ectoparasites straight from the skin of the groomee while the hands are used to hold the hair apart, or for balancing. The choice of body part to be groomed may be decided by either individual. Sometimes the groomee presents a part of the body they wish to have groomed to the groomer (Goodall 1968), and at other times the groomer chooses the body part to be groomed and moves it into place. Grooming often lasts a long period of time and individuals swap roles from groomer to groomee, but shorter grooming bouts and one-sided grooming or group grooming are also common.

Self grooming involves only the groomer, who uses similar methods as for social grooming to groom themselves (Goodall 1968).

## **6.3 Factors affecting social grooming behaviour**

Many factors affect the choice of a grooming partner and the time spent grooming by individual chimpanzees. Generally an individual chooses a partner that they

already have a close, supportive relationship with or an individual with whom a better relationship would be an advantage (Goodall 1986); but there are other factors involved. For example, the dominance, sex and age of an individual can have an impact on whether two particular individuals will groom together. Association levels, specific relationships (e.g. kinship), the oestrous state of a female, the effect of injury and even the individual personality of the chimpanzee can have an impact on the time spent grooming and the choice of grooming partner.

## Sex

Choice of grooming partners differs for adult male and adult female chimpanzees. Grooming between adult males is common, and between adult females, less frequent. Nishida (1979) reported that 46% of total grooming time was spent between adult males, 39% between adult males and adult females, and 10% between adult females (it was mentioned that there was an observational bias, with more frequent encounters with core subgroups, and less encounters with family groups, this led to only 5% of observations to be with juveniles and infants) (Nishida 1979). The general pattern of grooming between adults reported by Nishida is similar for most other chimpanzee populations that have been studied (excepting Bossou), in that the grooming frequencies were higher than expected between adult males, and lower than expected between males and females, and between females (Boesch & Boesch-Achermann 2000; Muroyama & Sugiyama 1994). That males mostly groom with other males in a community reinforces the idea that bonds between males are central to chimpanzee sociality (Watts 2000a). Females on the other hand spend most of their grooming time, grooming family members (Goodall 1986). Mothers groom for around the same amount of time as adult males, but they direct a lot of their grooming to their offspring (Wrangham et al. 1992). Details of grooming behaviour between a mother and her infant, and the development of grooming behaviours in young chimpanzees can be found in Chapter Five (section 5.2.3). A female benefits from grooming her offspring by maintaining a close relationship with them so that they can provide her with support and companionship (Goodall 1986).



Studies from Bossou, Guinea, found that females groomed other females more often than they groomed males (Sugiyama 1988), which is in contrast to the results seen from other study sites. This difference may be because the Bossou community is isolated from other chimpanzee communities so the alpha male does not need to rely on a coalition of males as is seen in other populations. This leads to male bonds being less necessary, so male-male grooming is reduced (Sugiyama 1988). No chimpanzee community living in a more natural setting has been found with the same social patterns (Wrangham et al. 1992).

### **Dominance / Age**

Dominance rank affects the grooming behaviour of chimpanzees at Ngogo, Kibale National Park, Uganda, in two ways. High ranking males have more grooming partners than mid or low ranking males, and grooming is particularly common between males that are close in rank, and less common between those far apart in rank (Watts 2000b). The Ngogo population is much larger than any of the other chimpanzee communities that have been studied, having 24 adult males in mid-1999 (Watts 2000a). No other studies have shown such a consistent relationship between dominance rank and grooming (Watts 2000b), although Simpson (1973) found that the male chimpanzees at Gombe National Park, Tanzania, who groomed most frequently and/or groomed for longer had a higher status (Simpson 1973).

At Taï Forest it was at first found that age, rather than rank, played a significant role in grooming between adult males, but five years later when the study was repeated rank, rather than age, had now become the most important factor affecting grooming (Boesch & Boesch-Achermann 2000). So the period in which communities are observed may influence results, as well as the individual personalities within the community at any given time.

Dominance rank is less obvious in adult female chimpanzees, than in adult males. As grooming is rare amongst adult females very little is mentioned about the influence of dominance and age on their grooming patterns. However in vervet monkeys (*Cercopithecus aethiops*), a species where female-female grooming is

common, there is a significant positive correlation between a female's rank and the total amount of grooming she received from others (Seyfarth 1980).

### **Association**

Association between individuals may affect the tendency for grooming between individuals, in that two individuals may be more likely to groom if they associate a lot together. The fission-fusion social organization in chimpanzees means that not all individuals in a community are available for grooming at any one time; in fact it may be days, and even weeks, before some individuals encounter each other. Adult male chimpanzees in the Tai Forest have been found to groom males more with whom they associate more frequently (Boesch & Boesch-Achermann 2000). Many factors affect association levels (see Chapter 4) and thus also indirectly affect levels of grooming.

### **Oestrous state of females**

When an adult female is in oestrus, the length of time that one adult male stays near to her is longer than when she is not in oestrus (Matsumoto-Oda 1999). If association were a factor affecting grooming then it would be assumed that when adult females are in oestrus they would receive more grooming from males. Also if a male were trying to attract the favour of the female, it is possible that he may use grooming to do so. There are conflicting results. In one study females were groomed more by males when in oestrus than at other times (Goodall 1986), in contrast another study found no difference in the time males spent grooming oestrous and anoestrous females (Matsumoto-Oda & Oda 1998). A further study found when males show possessiveness for an oestrus female, or when males are on consortship with an oestrus females, they spend more time in the same group with her, and more time grooming and sharing food with that female (Tutin 1980).

Grooming may be affected by sexual behaviour in that females prefer consort and mating partners with whom they have shown high frequencies of grooming and sharing food behaviour during non-sexual contacts (Matsumoto-Oda 1999; Nishida 1988). Different lactational states of the female may also affect the

grooming behaviour of females. The increased energy demands associated with lactation and infant transport can reduce the amount of time that is available for grooming (Watts 2000a). Grooming is also affected by the stage of the swelling cycle of the female. In a captive study it was found that males initiated grooming more as the females cycle progressed from the luteal to the follicular phase, with peaks during the days of the swelling onset, and again when the female was menstruating (Wallis 1992).

## **Injury**

Two studies have looked into the effect of injuries on grooming behaviour in chimpanzees. The first study used data collected from the present study site, Budongo Forest, and found that hand injuries did not affect the pattern in which an individual performs or receives grooming (Spini 1998). Although these were only preliminary findings it was shown that injured individuals form part of the grooming network. It was also suggested that when chimpanzees with hand injuries are the groomers, the hygienic role of the function of grooming might be reduced because of their paralysed fingers (Spini 1998). The second study, also from Budongo Forest, recorded the extent of disability in injured chimpanzees and found a lower capability in social and self grooming for the three injured mothers with hand injuries: Kalema, Keway, and Zana (Stokes 1999).

### **6.4 Aims of this chapter**

The aim of this chapter is to determine whether injured adult female chimpanzees of the Sonso community are able to groom effectively, and if so, whether they groom to the same extent as non-injured adult females.

If a chimpanzee has significant injury to one or both hands, grooming would be restricted to the use of the good hand, or digits. If a chimpanzee has injuries to either the hands or feet, balance required for a long grooming session may be difficult, particularly in arboreal space. A lower level of grooming for injured chimpanzees may be likely if this was the case.



Chapter Five has outlined how mothers with injuries are able to care for their dependants. Grooming is another behaviour where there may be differences between injured and non-injured mothers. Injuries may make grooming more difficult for mothers, so they may groom less. In contrast it may take mothers longer to groom their offspring effectively, and so they may spend more time grooming them. Dependants of injured mothers may spend longer grooming their mothers as a way of assisting them if the mother has difficulty in self grooming, or is rarely groomed by other individuals.

Social grooming with community members other than dependants may also be affected by injury. A low level of grooming others may be seen in injured chimpanzees if they are physically unable to groom, or have difficulties in doing so. Also, since grooming has been found to be related more to social complexity than hygiene (Dunbar 1988), it is possible that if injured chimpanzees are less tolerated or socially isolated in the community then they will be groomed by other community members less than non-injured chimpanzees. So if injured mothers are grooming others, this suggests they are physically able to groom; and if other community members are grooming an injured mother, this suggests a level of social acceptance within the community.

The number of grooming partners may be affected by injury if injured chimpanzees are less social than non-injured chimpanzees, or less tolerated by other community members. I also hypothesise that injured chimpanzees would spend more time self grooming to compensate for any reduced social grooming, and because effective grooming may take longer.

## **6.5 Methods**

### **6.5.1 Definition of terms**

Grooming bout: is defined as any social grooming between individuals (including grooming, being groomed, pair and group grooming) that lasts more than 10 seconds, and is not interrupted by another behaviour for more than 10 seconds.  
Mutual grooming: two chimpanzees grooming each other at the same time.

Group grooming: three or more chimpanzees involved in grooming each other. Group grooming has been analysed as if there was two separate grooming bouts. For example if Kwera was grooming Black, while Kwezi was grooming Kwera for a period of 38 seconds, each pair is recorded as group grooming for 38 seconds each.

Self grooming: one chimpanzee grooming itself.

Grooming “others”: others are defined as all community members apart from the offspring dependant on the mother (these offspring include the youngest dependant and any older juvenile offspring).

### **6.5.2 Descriptions of grooming and mother-dependant grooming**

Ad-lib sampling was used to describe the different methods of grooming used by females with injured hands at Sonso. Focal animal sampling (Altmann 1974) was used to collect data on mother-dependant grooming behaviour during half hour observation periods. Percentages (out of the time spent social grooming) were calculated in order to find trends in the data. Statistical analysis follows the two-stage approach to modelling outlined in Chapter Three and briefly described below. This method was used because the data set contained many observation periods where either no dependant grooming occurred, or dependant grooming took up the total time spent in social grooming; this type of data has no variation. Injury status of the mother, season, age of dependant and presence of an older sibling were factors used in the model. Sex of dependants was not included as 75% of dependants were female, and only one infant was male. The Bonferroni correction method was used for multiple comparisons (see section 3.5.2) with a resulting significance level of 0.025.

### **6.5.3 Grooming interactions with the rest of the community**

Focal animal sampling (Altmann 1974) was used to collect data on adult female grooming behaviour involving other community members during half hour observation periods. Grooming behaviour in female chimpanzees is known to be low with respect to grooming other community members (section 6.3). This was the case in this study, leading to a large number of zero observations in the data



set and the use of a two stage approach in the analysis (see section 3.5.3). The first stage uses a binomial GLM to determine whether there is a significant difference in the probability of the occurrence of a particular behaviour in observation periods. If there is a difference then only observation periods where the behaviour occurred are included in the second stage of the analysis in order to determine whether there was a significant difference in the time spent in the behaviour being analysed. The factors that were included in the analysis were injury status of the mother, season, dependant age, and time of day. A test for a difference in two binomial proportions (Z-test) was used for mutual and group grooming data (see section 3.5.3), using only observation periods where some kind of social grooming occurred (total of 200 half hour samples). The Bonferroni correction method was used for multiple comparisons (section 3.5.2) with a resulting significance level of 0.01. This significance level has been used in all analyses, but where results would have been significant to the 0.05 level, exact significance levels are stated in order to examine general trends in the data.

#### **6.5.4 Grooming partners and self grooming**

Focal animal sampling (Altmann 1974) was used to collect data on grooming partners and time spent self grooming. Frequencies and percentages were then calculated in order to examine trends seen in the data. Statistical analysis was not used for data on grooming partners as there was a large proportion of the data where no grooming partners were recorded, and where recorded they were in low numbers. As there were many observation periods where no self grooming occurred, the two stage approach to modelling (outlined in section 3.5.3) was used.

### **6.6 Results**

#### **6.6.1 Grooming methods used by injured chimpanzees of the Sonso community**

Chimpanzees with injured hands use modified forms of the grooming style described in section 6.2. Chimpanzees with injuries to the feet use the same



grooming methods as non-injured chimpanzees (so are not described below) but they have the added difficulty of balancing with one less foot available for grasping. This was particularly noted for Kigere who was missing a whole foot: she was observed to threaten younger chimpanzees who played near her and moved the branch she was balancing on. Kigere has also been described losing her balance when travelling in arboreal space (see section 7.6.1).

The following are the methods of grooming used by Sonso chimpanzees with injuries to their hands. A study on wild chimpanzees from Tai National Park indicates that adult chimpanzees are highly lateralized for complex tasks, but there is no bias towards either right- or left-handedness in the population (Boesch 1991). This suggests that chimpanzees are equally likely to be right or left handed, and so it is not possible to determine if the following individuals have injuries to their preferred-use hand.

#### **Kalema (right hand injured)**

Kalema grooms mostly with only her left hand. She was observed to groom herself with her right hand on rare occasions where she ran the back of the right hand over her hair enabling the hair to be parted very coarsely. On one occasion she was observed scratching herself with her mangled fingers. When using her left hand, she uses the same techniques as able-bodied chimpanzees.

When grooming her dependant she uses only her left hand. Her injured hand is either used for stability or is just held out the way. I have seen her use her right hand as a hook over a branch to steady herself while she is grooming. She uses both feet and sometimes her injured hand to balance when grooming in the trees.

#### **Zana (both hands injured)**

Zana has injuries to both hands, and she attempts to use both in order to groom herself, but only her right hand is used to groom her juvenile.

When grooming her dependant the left hand is used to hold him in place or for her balance, while the right hand is used for grooming. The injury that Zana has on her right hand leaves her with one finger and a thumb that she has use of and it is these digits (mainly the finger) that she uses to both part her juvenile's hair and to pick off any foreign articles. She often uses her finger to move the hair and her mouth to pick the foreign articles away. She appears to use her mouth in grooming her dependant more than any other of the females.

When self grooming she uses both hands, using the one finger on her right hand to move through the hair, and using the back of her left hand or rubbing the floppy fingers of her left hand along her body to part the hair. Other methods of self grooming include using a foot to groom under her arm and stomach, and using branches to scratch her back and the inside of her arms and shoulders.

#### **Kewayaya (right hand injured)**

Kewayaya has been observed to groom other community members with her left hand only. When grooming her infant she holds her in place with her right hand but grooms with her left. When self grooming she uses her left hand mostly, but sometimes the back of the right hand is used to scratch. She rubs against branches in order to scratch the back and inside of her arms and shoulders.

When grooming socially with Zimba (most common grooming partner, and thought to be her mother) there were many times that Kewayaya had to use her good hand to balance, during a grooming session in arboreal space, rather than reciprocate grooming to Zimba (see description at beginning of this chapter).

#### **6.6.2 Grooming between the mother and her dependant**

On average, adult female chimpanzees, whether injured or not, in this study spent 62.5 % of their total grooming time grooming their young offspring (including youngest dependant and older juvenile siblings), or 6.3 % of the total time they were observed. These results fall within the range of mother-infant grooming seen in the other studies (Assersohm 1999; Pusey 1983).

### **Mother grooming dependant**

When comparing by injury status it was found that injured mothers groomed their dependant offspring for an average of 70.2 % of their total grooming time whereas non-injured mothers groomed theirs for an average of 57.0 %. It must be noted that some mothers have more than one offspring, and this is known to affect the total time spent grooming offspring (Nishida 1988). In this study mothers with two dependant offspring groomed them for an average of 68 % whereas mothers with one dependant offspring groomed it for 58.5 % on average. Five mothers had an older juvenile dependant, one of these mothers is injured and four are non-injured mothers. The following analyses were conducted on the amount of time a mother spent grooming her youngest dependant only, and the presence of an older juvenile sibling was included as a factor in the model. So, as for Chapter Five, the term 'dependant' refers to the youngest dependant (which includes all Infant 1, Infant 2, and Juvenile 1) in the analysis of mother-dependant grooming.

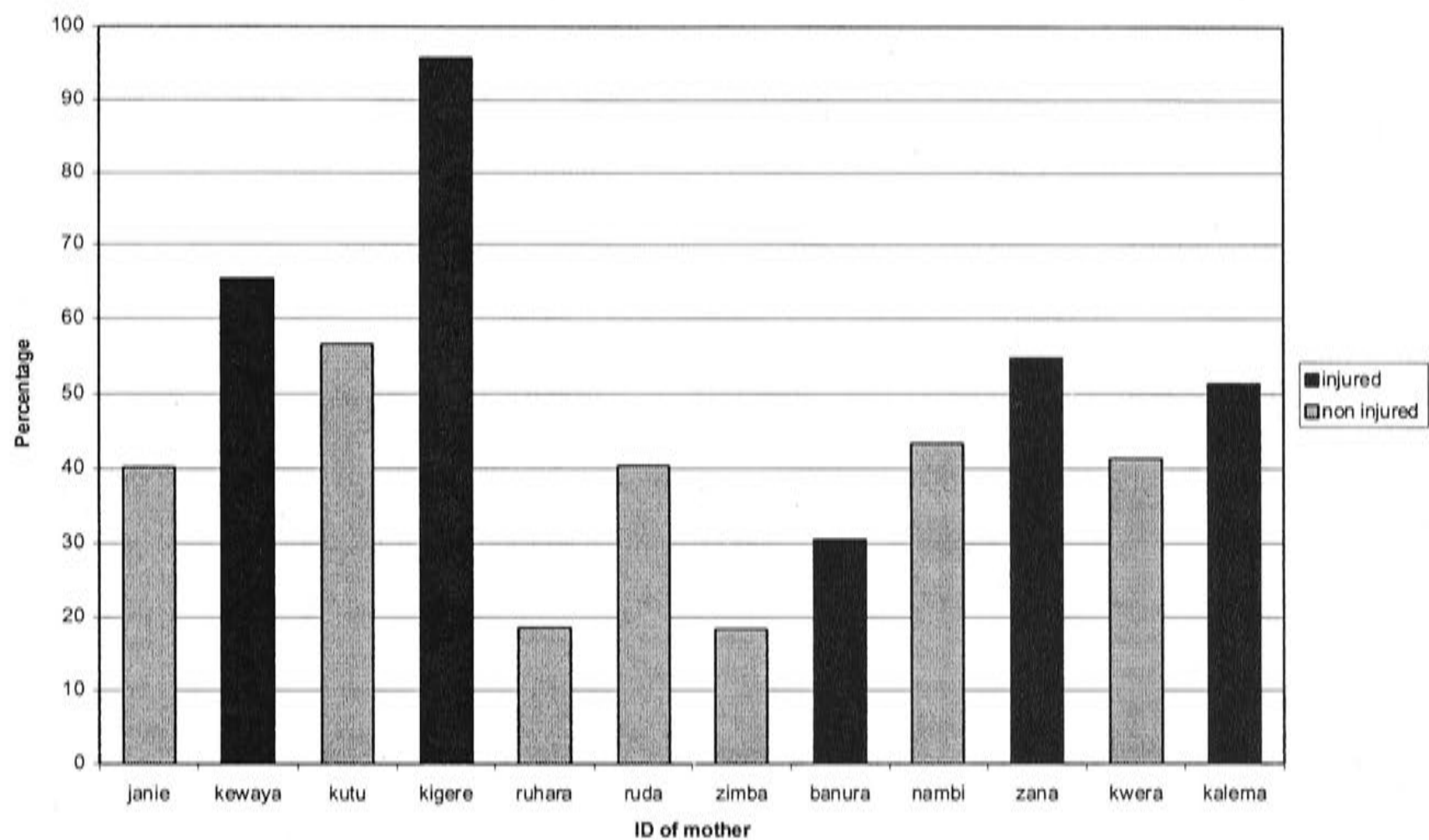
The percentage of time a mother spent grooming her dependant (out of the total time a mother spent in social grooming) was calculated and is summarised in Figure 6.1. As for graphs in previous chapters the mothers are ordered from left to right with those with the youngest dependants on the left and those with the oldest on the right.

Figure 6.1 shows no clear trend in the time a mother grooms her dependant and the age of a dependant, or the injury status of the mother. Younger and older dependants do seem to be groomed more if they have injured mothers, but this is not the case for the dependants of intermediate age.

A binomial GLM revealed a significant association between the probability of a mother grooming her dependant and dependant age ( $F=4.54$ ,  $d.f.=2,195$ ,  $p<0.025$ ). The probability of a mother grooming dependants is greatest for Infant 1, less for Juvenile 1, and least for Infant 2. No effect of injury ( $F=2.09$ ,  $d.f.=1,190$ ,  $n.s.$ ), or any other factors included were seen.



**Figure 6.1** Time spent grooming dependant as a percentage of mother’s time in social grooming (for all figures in this section refer to Table 3.6 for number of observation periods and total time observed for each focal subject)

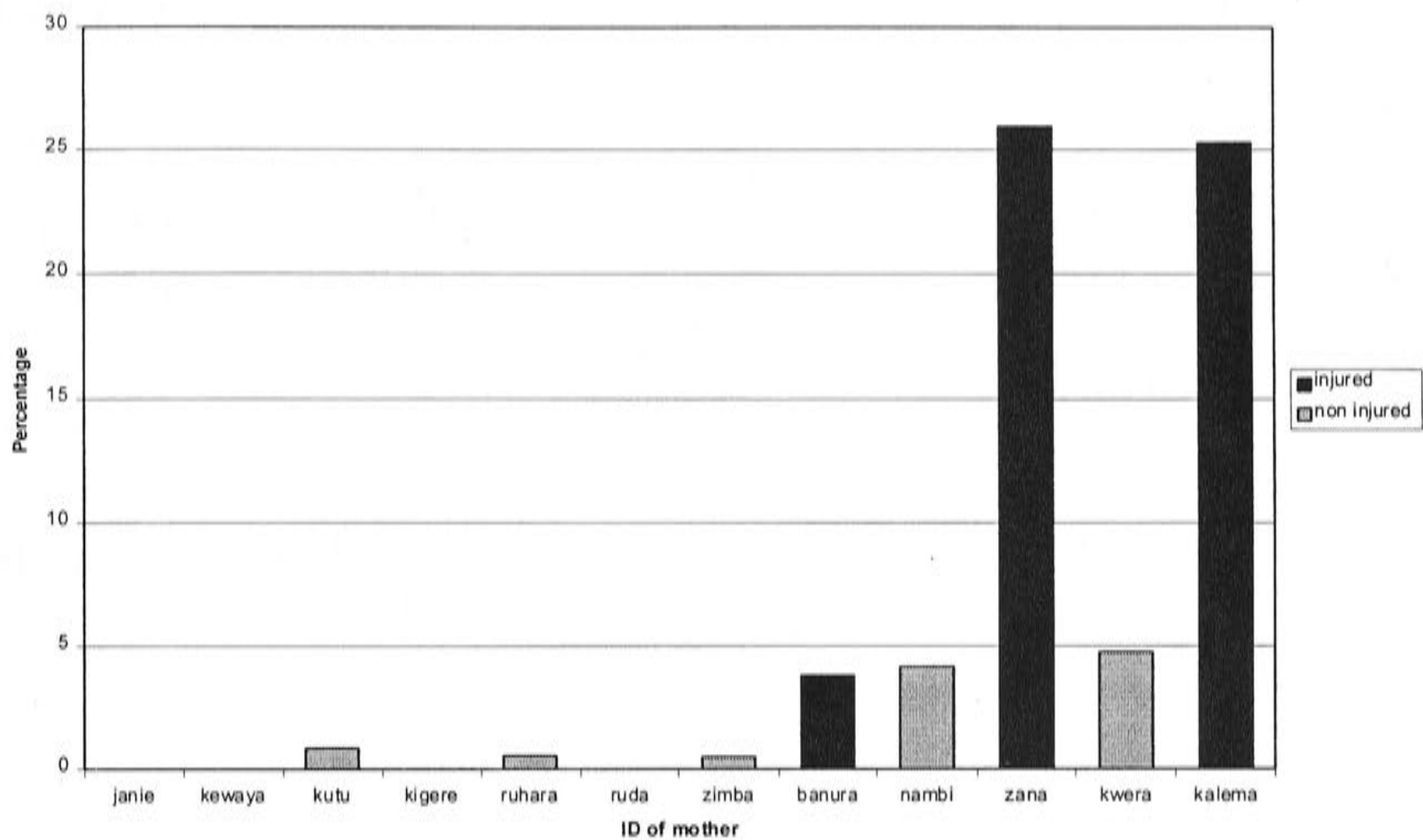


**Mother groomed by dependant**

Figure 6.2 shows the percentages of social grooming time that a mother was groomed by her dependant.

When looking at Figure 6.2 it can be seen that the percentage of time that a dependant groomed its mother was highest for the two juveniles with injured mothers (Zana and Kalema), their values were extremely high when compared to juveniles of the same age with non-injured mothers. Infants (Janie to Banura) spent very little, or no time grooming their mothers as would be expected for young chimpanzees. In order to examine a juvenile’s role in the grooming of the mother, older juvenile siblings (see Table 5.1) were added, and infants were removed from the analysis. Table 6.1 lists the juveniles used in the analysis and

**Figure 6.2** Time dependant groomed mother as a percentage of the mother’s time in social grooming



**Table 6.1** Amount of time juvenile offspring groomed mother as a proportion of the amount of time mother spent in social grooming

<i>Mother / offspring</i>  <i>(Injured individuals are in bold)</i>	<i>Age class of offspring</i>	<i>Number of injuries of mother</i>	<i>G - Amount of time grooming mother</i>	<i>T - Total time mother spent in social grooming</i>	<i>G / T (%)</i>
Ruda / Bob	Juvenile 2	-	0:13:22	1:29:56	14.86
<b>Banura / Shida</b>	Juvenile 2	1	0:19:49	1:57:59	16.80
Zimba / Gonza	Juvenile 2	-	0:16:33	3:56:59	6.98
Nambi / Musa	Juvenile 2	-	0:08:49	1:35:07	9.27
Kutu / Kato	Juvenile 2	-	0:03:57	1:11:14	5.55
<b>Kalema / Bahati</b>	Juvenile 1	1	0:21:38	1:25:23	25.34
Kwera / Kwezi	Juvenile 1	-	0:10:58	3:50:40	4.75
<b>Zana / Zalu</b>	Juvenile 1	2	0:26:11	1:40:48	25.98
Nambi / Nora	Juvenile 1	-	0:03:58	1:35:07	4.17

the amount of time they groomed their mother as a proportion of the total time their mother spent in social grooming. Note that one mother (Nambi) has two juvenile offspring so is included twice in this analysis.

Table 6.1 shows that the three juveniles with injured mothers spent the largest proportion of time grooming their mothers (mother-dependant pairs are in order by age of offspring, the oldest juvenile appearing at the top of the table). The same two juveniles (Bahati and Zalu) with injured mothers still spent much longer grooming their mothers than all other juveniles, even though they are younger than many of the other juveniles. Shida had an injured mother and spent a relatively large amount of time grooming her mother, but not much more than Bob, who does not have an injured mother. Shida also has severe injuries (see Figure 2.7); it is possible that she is unable to groom her mother as much as Bahati and Zalu, as she is missing one hand, and has a snare on one foot, therefore the amount of time she is seen to groom is likely to be lower than expected because she herself is injured. However, it is difficult to say whether Shida is grooming at a lower rate overall since many juveniles with non-injured mothers groomed their mothers for less time than Shida, despite her injuries. Shida's grooming is only low on comparison to the other juveniles with injured mothers.

Using only data from when social grooming occurred a binomial GLM found no significant association between the proportion of time a mother was groomed by her juvenile and her injury status ( $F=0.03$ , d.f.=1,137, n.s.). Age of the juvenile and season were also factors used in the model, and neither affected the results shown.

Since Shida is also injured, and it is possible that the time she spent grooming her mother is lower than expected, the analysis was repeated removing Banura/Shida from the data set. No significant difference was found ( $F=0.03$ , d.f.=1,125, n.s.). Although the raw means above suggest that juveniles with injured mothers groom them more, statistical analysis does not show this relationship. This is clearly because removing Banura/Shida from the data leaves only two injured chimpanzees in the analysis, leading to a large standard error. When Banura is

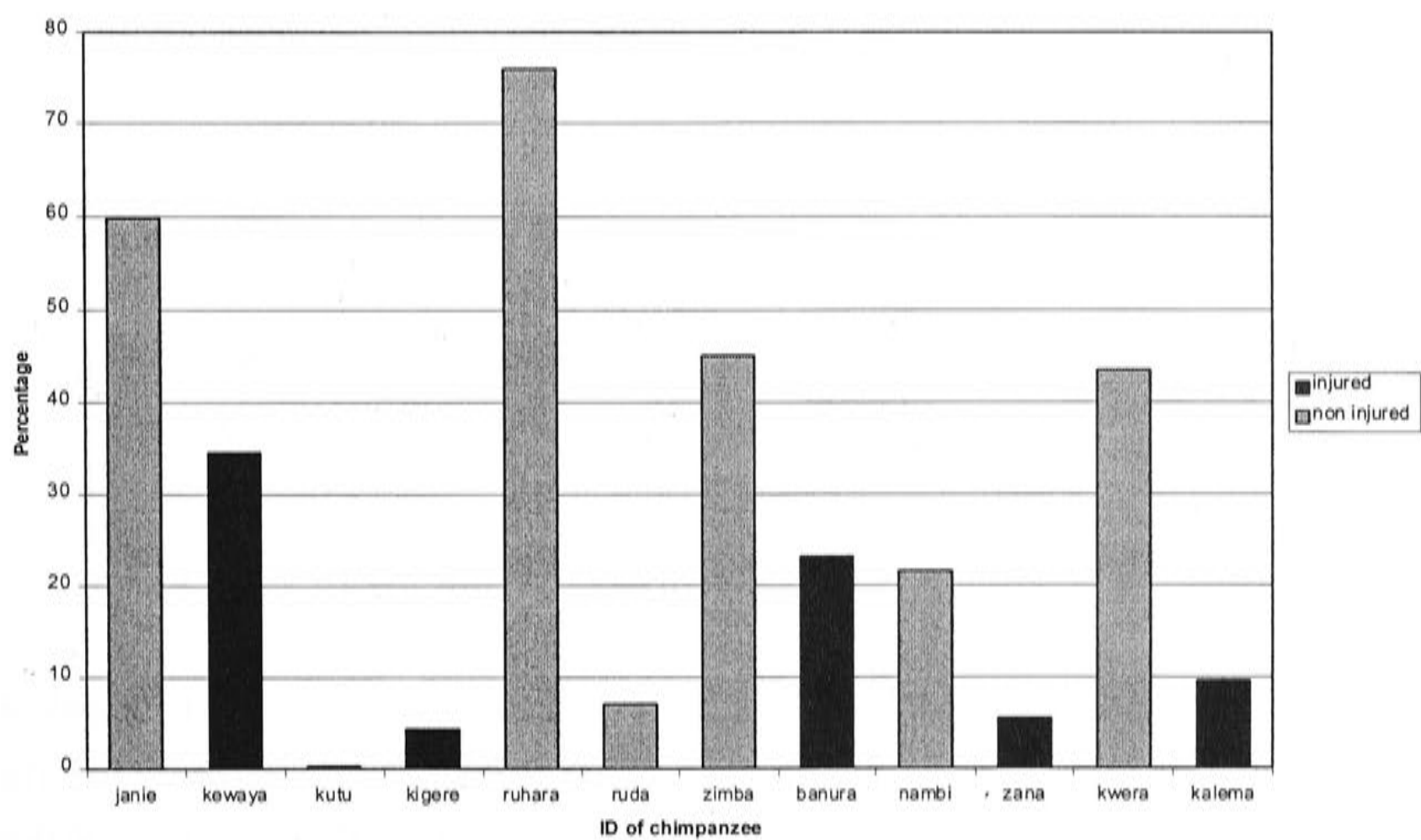


included in the data the difference between injured and non injured is not clear enough to suggest any significant difference.

6.6.3 Grooming interactions with the rest of the community

Figure 6.3 looks at the total time a mother spent grooming others in the community as a percentage of the total time she spent in social grooming. ‘Others’ refer to all community members except youngest dependants and older juvenile offspring of the focal subject (see section 6.5.1). The percentage of total social grooming time that each female was in grooming behaviour with other community members shows variation, ranging from less than 1% to 76% (see Figure 6.3). The amount of time each individual spent in social grooming behaviour with others also varies, ranging from 17 seconds (Kutu) to 1 ¾ hours (Zimba). It appears from Figure 6.3 that non-injured mothers have the highest levels of social grooming, but there are non-injured mothers with very low levels as well.

**Figure 6.3** Time spent in social grooming with other community members as a percentage of total time spent in social grooming



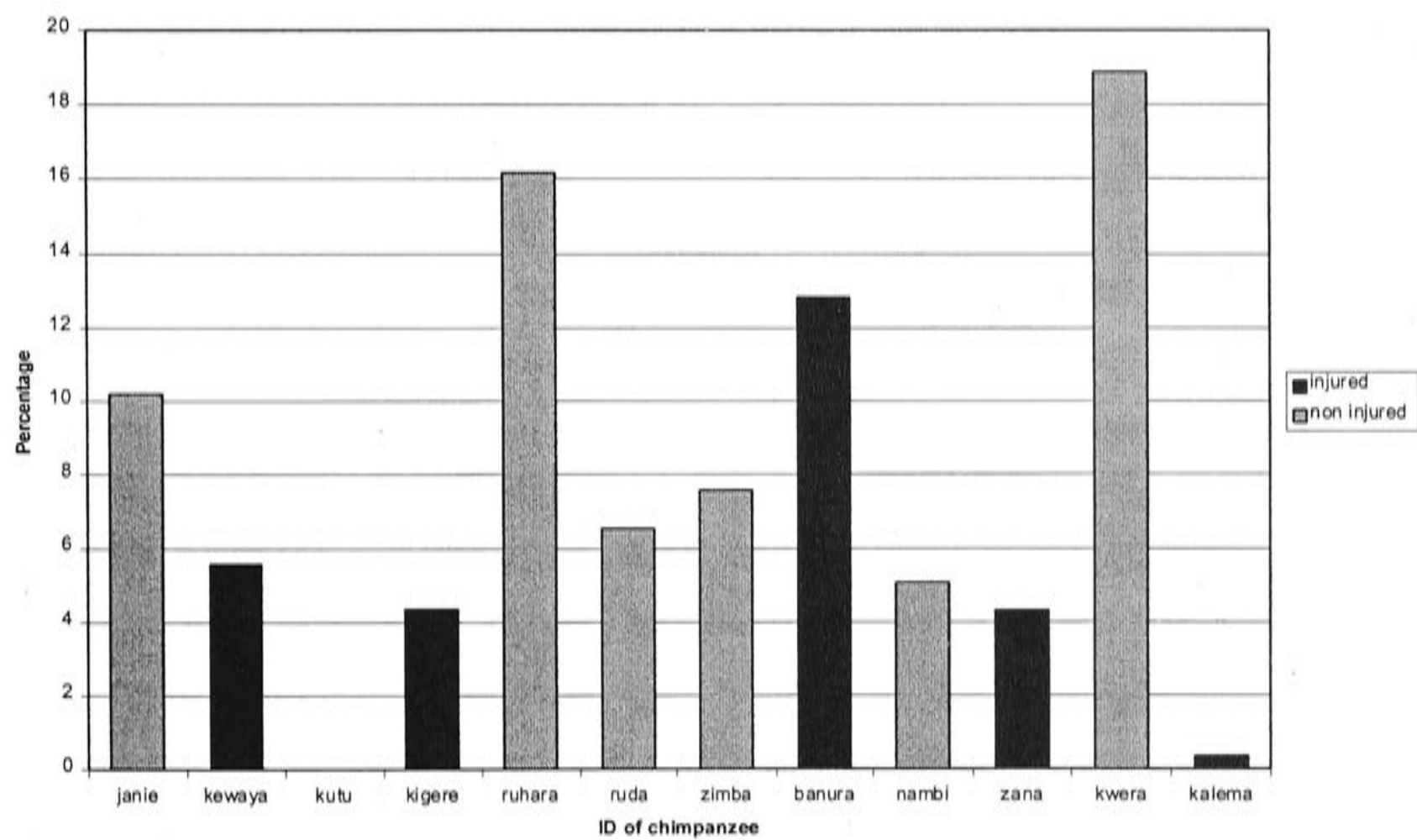
Social grooming can be divided up into four categories: grooming others, being groomed by others, mutual grooming and group grooming. Each category will be

analysed separately in order to determine whether any differences can be found between injured and non-injured chimpanzees.

Grooming others

Figure 6.4 shows the percentage of time each focal subject spent grooming other community members. Two individuals groomed others for less than 1% of their time in social grooming, one was injured and one not injured. There seems to be a lot of variation in the data between focal subjects, and no difference between injured and non-injured. Type of injury also does not seem to be playing a role, as Zana, with two hand injuries groomed others for more time than Kalema, with one hand injury, and Kutu, with no injury.

**Figure 6.4** Time spent grooming others as a percentage of total time in social grooming



A binomial GLM revealed that the injury status of the mother significantly affected the probability of whether grooming others occurred ( $F=9.30$ ,  $d.f.=1,446$ ,  $p<0.005$ ). The probability of grooming others occurring was significantly lower for injured chimpanzees, than non-injured chimpanzees.

All chimpanzees showed a trend in the likelihood of grooming at different times in the day ( $F=4.37$ ,  $d.f.=1,446$ ,  $p=0.039$ ), with the probability of grooming in the morning hours greater than in the afternoon hours. Season and age of dependant had no effect on the results.

The second stage of the analysis, using a linear mixed model, revealed that there was a significant association between the amount of time spent grooming others and both the combined effect of injury and season (Wald statistic=7.68,  $d.f.=1$ ,  $p<0.01$ ) and the effect of time of day (Wald statistic=6.85,  $d.f.=1$ ,  $p<0.01$ ).

On combining the two stages of the analysis the results show that injured chimpanzees were less likely to groom others, but in the wet season they spent more time grooming others than non-injured chimpanzees, and in the dry season they spent significantly less time grooming others than non-injured chimpanzees. Both injured and non-injured individuals spent longer grooming others in the afternoon, but the probability of grooming others was greater in the morning.

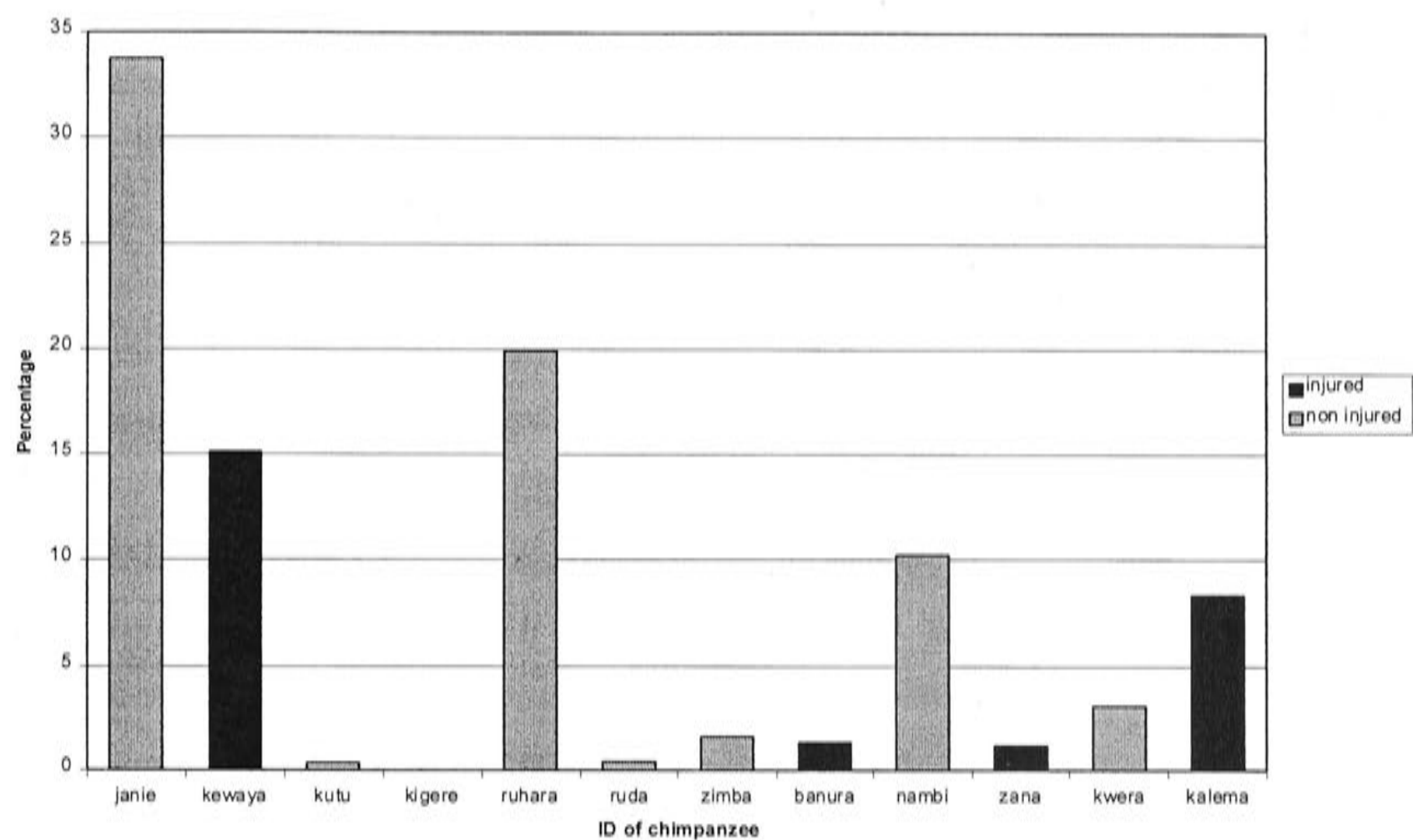
### **Being groomed by others**

Figure 6.5 shows the time mothers were groomed by other community members, as a percentage of the total time they spent in social grooming. Once again non-injured chimpanzees had the highest percentages of time being groomed by others, but variation still exists for all individuals.

A binomial GLM revealed that the time of day significantly affected the probability of being groomed by others ( $F=9.23$ ,  $d.f.=1,449$ ,  $p<0.01$ ). All focal subjects were more likely to be groomed in the morning hours than in the afternoon hours. No significant effect was found for any other factors included in the model. As there was no difference found for injured and non-injured individuals, the second stage of the analysis involving time spent being groomed by others was not carried out.



**Figure 6.5** Time spent being groomed by others as a percentage of total time in social grooming



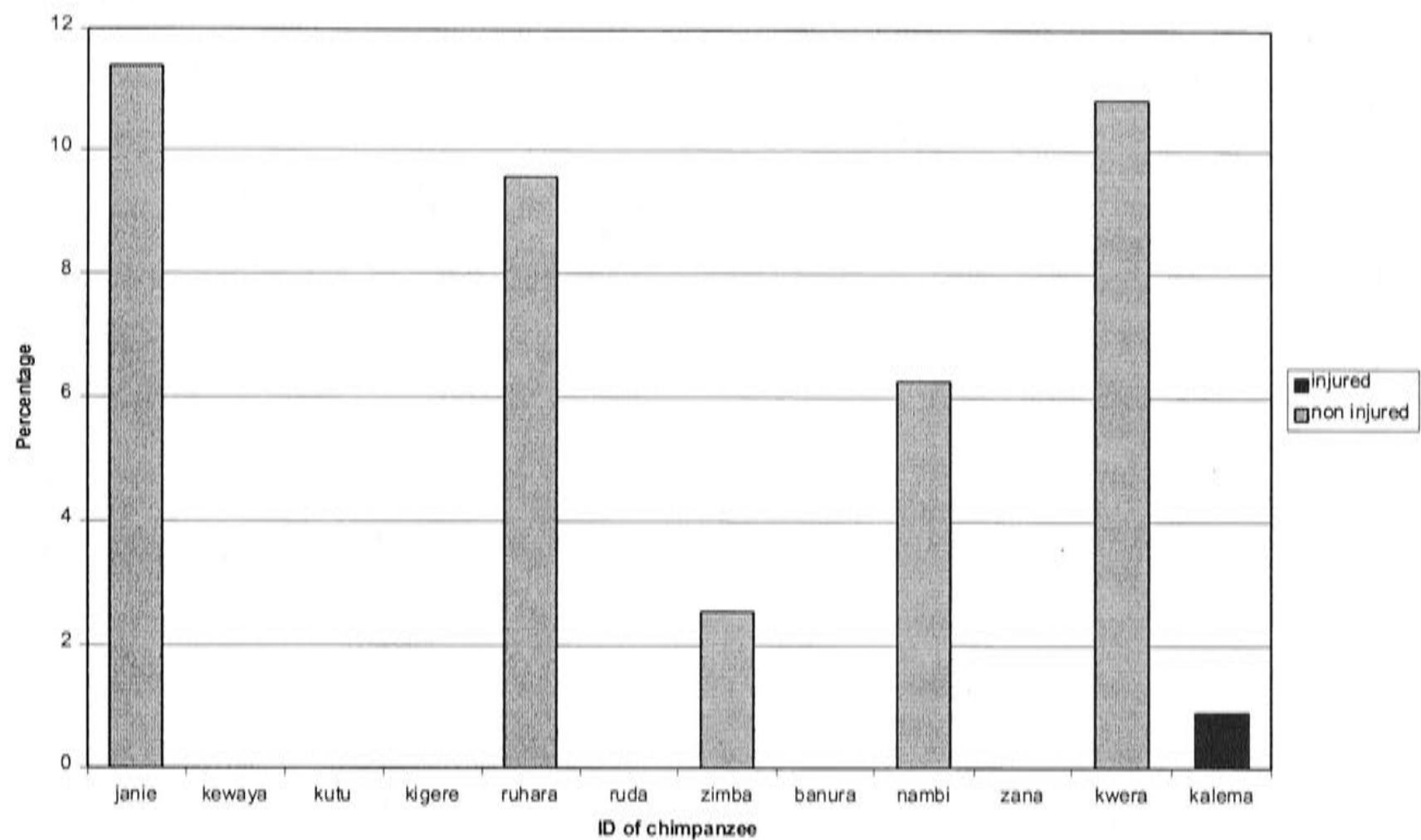
**Group grooming and mutual grooming**

Group grooming and mutual grooming with other community members were observed less frequently than other grooming behaviours for all study females. Figure 6.6 shows the percentage of time spent in group grooming. Most injured females, and some non-injured females, were not observed to group groom with others. For those who participated in group grooming, levels were higher for the non-injured females when compared to the injured female.

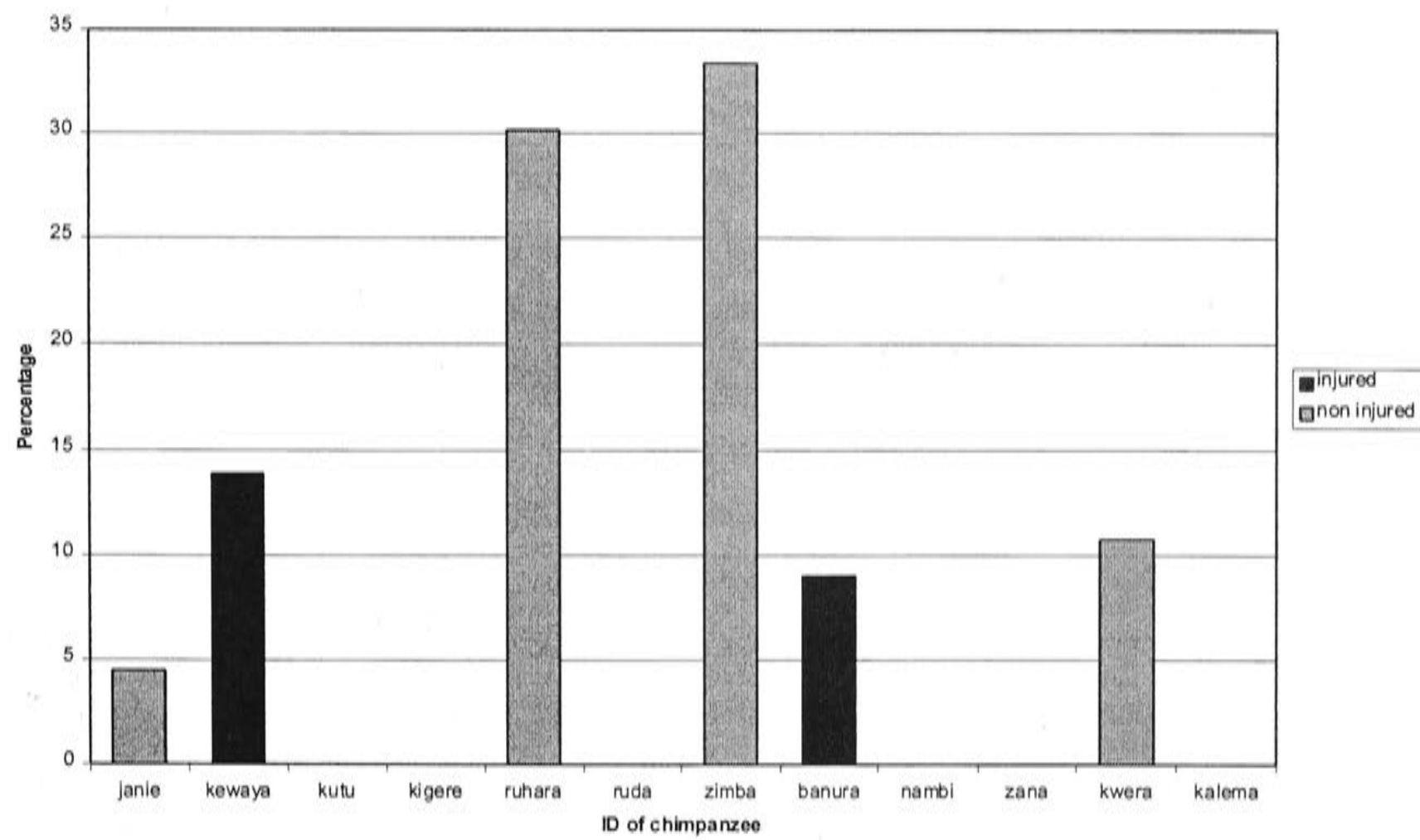
When testing for a difference in two binomial proportions a significant difference was found between injured and non-injured females for the probability of group grooming occurring ( $Z=2.89$ ,  $p<0.01$ ). Injured females are significantly less likely to engage in group grooming when compared to non-injured females.

Figure 6.7 shows the percentage of time spent in mutual grooming with other community members. Mutual grooming was highest for the few non-injured females that were involved in this behaviour.

**Figure 6.6** Time spent group grooming as a percentage of total time spent social grooming with other community members



**Figure 6.7** Time spent mutual grooming as a percentage of total time social grooming with other community members



A significant difference was found between injured and non-injured females for the probability of mutual grooming occurring ( $Z=2.51$ ,  $p<0.01$ ). Injured females

are significantly less likely to engage in mutual grooming when compared to non-injured females.

### **Number of grooming partners**

Grooming behaviour can also be analysed in terms of the number of grooming partners for each individual. The following tables summarize the number of grooming partners of each age/sex class in each of the four grooming behaviours. Since there were many occasions when no grooming partners were observed, there were many results of zero. These zeros are not included in the tables to allow results to be seen more clearly. Blank spaces therefore correspond to no grooming partners observed.

Table 6.2 looks at grooming other individuals and shows that only one injured female, Banura, had an adult male as a grooming partner. That individual was Zefa, who is presumed to be her adult son. In contrast, four of the non-injured females had between one and six different adult male grooming partners, and only one of these grooming partners was thought to be related (Nambi grooming her son Muga). Injured and non-injured females had around the same number of grooming partners for other age/sex classes.

Table 6.2 also looks at the number of grooming partners, but for when other community members were grooming focal subjects. Two injured females had one adult male partner; on both occasions this was Zefa who was low ranking and thought to be related to one of them. Four of the non-injured females had between 1 and 3 unrelated adult male partners. Of these adult male grooming partners seven were of the highest ranked individuals (Duane, Black, Jambo, Maani); the remaining one was low ranking (Andy). The only difference in number of grooming partners for other age/sex classes was that non-injured females had more sub-adult grooming partners than injured females.



**Table 6.2**      Number of grooming partners (not including youngest dependant and older juvenile siblings) when focal subject was involved in grooming and being groomed

<i>Focal subject</i> <i>(Bold injured)</i>	<i>Number of grooming partners when grooming others</i>					<i>Number of grooming partners when being groomed by others</i>				
	AM	AF	SAM	SAF	JAI	AM	AF	SAM	SAF	JAI
<b>Banura</b>	1	3	1		1	1				1
<b>Kewayya</b>		1					2			
<b>Kalema</b>			1			1	1	1		1
<b>Kigere</b>		1								
<b>Zana</b>							1			
Janie	6		1		1	3			2	2
Nambi	2	1				2	2			1
Kutu									1	
Kwera	4	4	1			1		1		
Ruhara	1	1	1			2		1		
Ruda		3	1					1		
Zimba		1					1			

AM – adult male

AF – adult female

SAM – sub-adult male

SAF – sub-adult female

JAI – juveniles and infants (not offspring of focal subject)

Table 6.3 looks at the number of grooming partners when focal subjects were group grooming with individuals other than their dependant offspring. Only one injured female was involved in any group grooming and this was with her juvenile daughter (Bahati) and a low-ranking sub-adult male (Nick). Five non-injured females were involved in group grooming with a total of 16 grooming partners; eight of these grooming partners were adult males (only one of these was related to a focal subject), three were adult females and four were sub-adults or juveniles (with one of the sub adults being related to a focal subject).

**Table 6.3**      Number of grooming partners (not including youngest dependant and older juvenile siblings) when focal subject was involved in group grooming and mutual grooming

<i>Focal subject</i> <i>(Bold injured)</i>	<i>Number of partners</i> <i>Group grooming</i>					<i>Number of partners</i> <i>Mutual grooming</i>				
	AM	AF	SAM	SAF	JAI	AM	AF	SAM	SAF	JAI
<b>Banura</b>						1				
<b>Kewaya</b>							1			
<b>Kalema</b>			1							
<b>Kigere</b>										
<b>Zana</b>										
Janie	3	1		1	1	2				
Nambi	2									
Kutu										
Kwera	3	1	1			1		1		
Ruhara		1	1			2		1		
Ruda										
Zimba		1					1			

AM – adult male

AF – adult female

SAM – sub-adult male

SAF – sub-adult female

JAI – juveniles and infants (not offspring of focal subject)

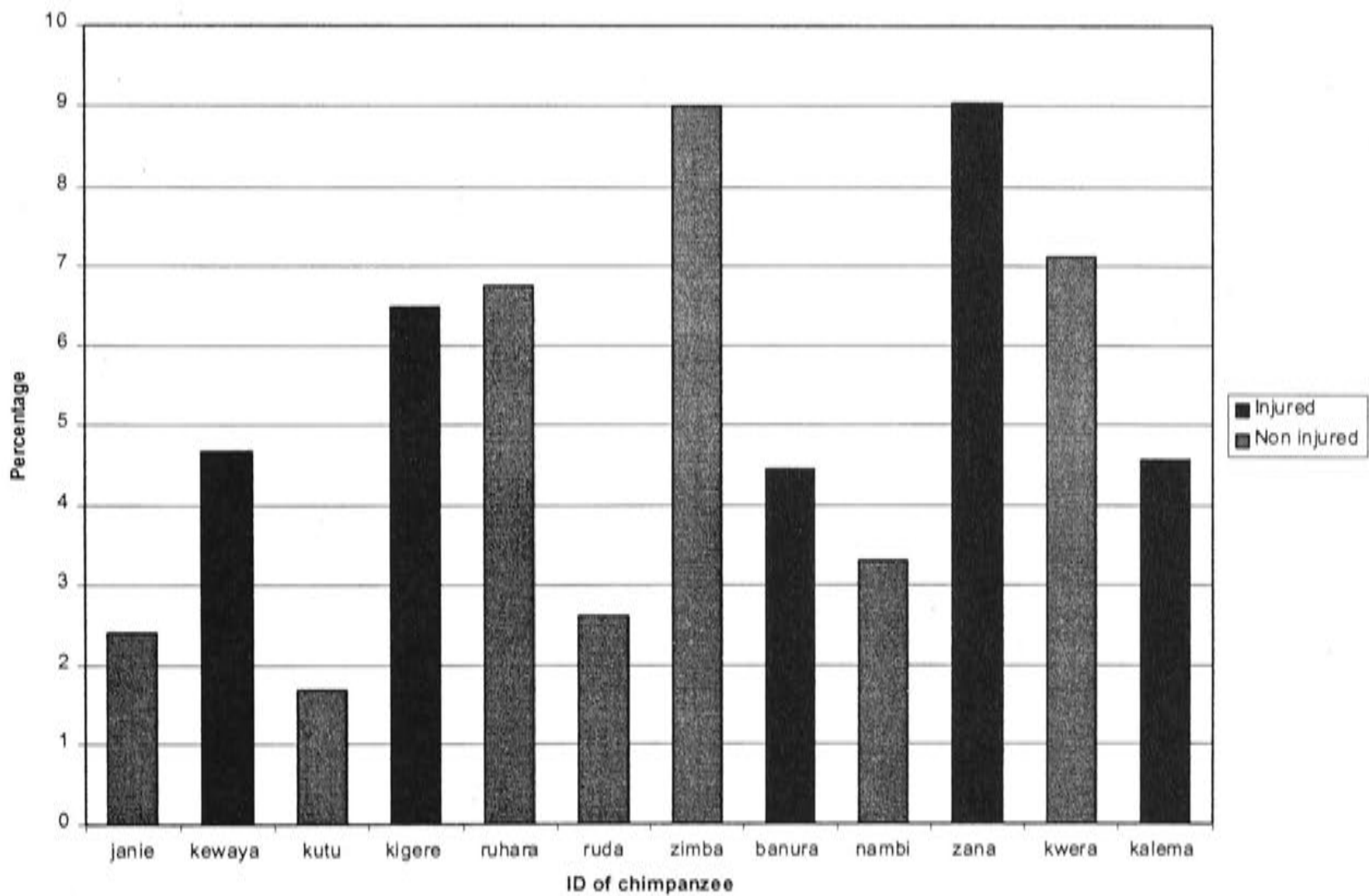
Table 6.3 also looks at the number of grooming partners when focal subjects were mutually grooming. Two injured females were involved in mutual grooming, both with related individuals. Four non-injured females were involved in mutual grooming. One of these (Zimba) had only one grooming partner who was thought to be her daughter (Kewaya), but the other three non-injured females had a total of five unrelated adult male partners (four of which were high ranking) and two sub-adult male partners (one of which was related).

It is noticeable from the above four tables that the same focal subjects in each table have the highest number of grooming partners and also the same individuals in each table have lower or no grooming partners.

6.6.4 Time spent self grooming

Figure 6.8 shows that there is a great deal of variation in the time spent self grooming between individual mothers. A binomial GLM revealed that no significant difference could be found for any factors that may have been affecting the probability of whether self grooming occurred. Factors included in the model were injury status ( $F=0.71$ , d.f.=1,447, n.s.), severity of injury ( $F=0.55$ , d.f.=2,448, n.s.), and season ( $F=2.13$ , d.f.=1,447, n.s.).

Figure 6.8 Percentage of time spent in self grooming



6.6.5 Summary of Results

- Chimpanzees with injuries to the hands groom using modified forms of grooming methods shown by able-bodied chimpanzees.



- No significant difference was found between injured and non-injured chimpanzees for mother and dependant grooming.
- Injured chimpanzees groom others in the community significantly less frequently than non-injured chimpanzees, although there is seasonal variation: in the wet season injured chimpanzees spent more time grooming others than non-injured chimpanzees, and in the dry season they spent less time grooming others than non-injured chimpanzees.
- No difference was found for time spent or the probability of being groomed by other community members for injured and non-injured chimpanzees.
- Injured chimpanzees are significantly less likely to group groom or mutually groom when compared to non-injured chimpanzees.
- Injured chimpanzees have fewer high-ranking, unrelated adult males as grooming partners than non-injured chimpanzees.
- There was no significant difference in the probability of self grooming for injured and non-injured chimpanzees.

## **6.7 Discussion**

### **6.7.1 Mother and dependant grooming**

There was no significant difference between injured and non-injured mothers in the time they spent grooming their dependants or the time their dependants groomed them.

It is quite possible that the time Shida spent grooming her mother was lower than expected (when compared to the results for the two other juveniles with injured mothers), and that if Shida were not severely injured she might have groomed her injured mother more often. If this had been the case the results may then have supported the idea that injured mothers are groomed more by their juvenile offspring. It was hypothesised that this may have been the case as a juvenile may be compensating for the mother having few grooming partners, or perhaps her inability to self groom effectively. This study found that other community

members groomed injured mothers as often as non-injured mothers, and that there was also no difference in self grooming; so there seems no need for a juvenile of an injured mother to have to compensate. It is possible that juveniles spent more time grooming their injured mothers simply because they spend more time in isolation with them, which was indeed the case in this study, where injured mothers spent more time in family groups, so alone with their offspring (see Chapter 4).

The possibility that juveniles with injured mothers groom them more is also supported by the fact that the two juveniles with the highest percentage of time spent grooming their mother were younger than many of the other juveniles. When comparing all the juveniles with non-injured mothers (see Table 6.1) a clear trend can be seen: older juveniles spent more time grooming their mother, and younger ones spent less. A previous study at Budongo Forest found that older infants groomed their mothers significantly more than did younger infants, and that juveniles groomed their mothers significantly more than infants (Assersohm 1999). Pusey (1983), in a study from Gombe, Tanzania, also states that infants groom their mothers more as they get older. Nishida (1988) found no correlation between the age of an infant and the amount of time spent grooming the mother (it was supposed that this might be due to a limited sample of observation hours), in a study at Mahale, Tanzania. A significant difference was found when comparing age of infant and the length of the grooming bout: length increased with age (Nishida 1988). It is then even more interesting that the levels of grooming undertaken by Zalu and Bahati were indeed so much greater than for all the other juveniles: relative to their age they would have been expected to groom their mothers for much less time.

### **6.7.2 Grooming interactions with the rest of the community**

#### **Grooming and being groomed by others**

The results show that there was no difference between injured and non-injured chimpanzees for being groomed by others in the community. There was a



difference seen for when injured chimpanzees were grooming others, they were less likely to do so than non-injured chimpanzees.

It is difficult to tell how the direction of grooming refers to the social implications of grooming. For instance adolescent male chimpanzees at Ngogo, Kibale National Park, spend much more time grooming adult males than being groomed by them (Sherrow 2001). This would suggest that grooming is a way for subordinates to be accepted socially by dominant individuals. This is not always the case; it has been shown at Mahale that the highest ranking individual is the one that grooms others the most (Takahata 1990), and also adult females spend little time grooming males (Nishida 1979). It is also difficult to determine from the available literature what the case may be for female chimpanzees, as female grooming is less commonly studied than male grooming. In this study I hypothesised that if injured mothers were grooming others, this was a measure of them being physically able to groom; and if other community members were grooming an injured mother, this was a measure of some level of social acceptance within the community.

Using this hypothesis, the results show that injured individuals are not socially isolated, as injured and non-injured mothers are both groomed by other community members to the same extent. Injured mothers are less likely to groom others, which implies that it may be physically difficult for injured chimpanzees to groom and so they engage in grooming less often. The physical difficulties may arise from having only one hand to groom with, but must also come from having one (or two) fewer limbs to use for balance, particularly in arboreal space, as two injured mothers have lower limb injuries only.

Season affected how much time mothers spent grooming others. In the dry season months, when food appeared to be scarce and more time was spent travelling in search of food (see Chapter 7), injured chimpanzees spent less time grooming others. It has been suggested elsewhere, for *Cebus apella*, that an increase in foraging time, because food was scarce, reduced the available grooming time (DiBitetti 1997). This may be the case for injured chimpanzees in this study. It is possible that the extra energy demands associated with factors such food scarcity



and increased travelling time affect injured chimpanzees to an even greater degree than non-injured chimpanzees, because of their injuries. During wet season months, when food appeared more plentiful and all individuals travelled less (see Chapter 7), injured chimpanzees spent more time than non-injured chimpanzees in grooming other community members, perhaps as a compensation for the lack of grooming at other times. Discussion and analysis of season in this thesis is only based on eight months: five during the wet, and three during the dry season. Although differences are found, they do not span an entire year.

Injured chimpanzees have been shown in Chapter Four to spend more time in small groups, and more time alone with their dependants, and so less time in large mixed sex groups. The fact that they spent less time in larger groups means that they have fewer opportunities for association with a larger number of individuals. It may be because of this factor that injured mothers are less likely to groom others, simply because they associate less with others, but this was not reflected in the time other community members spent grooming injured mothers. So physical difficulties in grooming are the more likely cause of injured mothers grooming others less often.

Although injured mothers groomed other community members less often, the same was not observed for grooming their dependants. It is possible that an injured mother is still likely to groom her dependants, despite physical difficulties, to the same extent as non-injured mothers as this is an essential part in the development and well being of their offspring. When it comes to other community members, if they are not groomed as often by injured individuals they will presumably seek out grooming elsewhere.

### **Group and mutual grooming with others**

Injured chimpanzees are less likely to mutually groom and group groom when compared to non-injured chimpanzees. Mutual grooming may be less common in injured chimpanzees, as it involves two chimpanzees grooming each other at the same time. Mutual grooming requires additional balance in arboreal space as, when grooming, chimpanzees have at least one less hand available to secure their

position. Injured chimpanzees might find balance more difficult as they have even fewer hands or feet available for grooming and grasping. If injured chimpanzees are less likely to groom mutually because of difficulties with balance, it is possible that many grooming sessions that would have been mutual become one-sided. This could inflate the results seen earlier for amount of grooming received by other community members. This was seen to be the same for injured and non-injured females, but perhaps should be less for injured females after all.

Group grooming may be less common in injured mothers because of difficulties with balance (as for mutual grooming) as it frequently involves a chimpanzee grooming one individual while being groomed by another. Group grooming could also be seen as the most social form of grooming, as it involves at least three individuals in a grooming party; it may then be less likely for injured chimpanzees since they are less social, spending more time in small groups and alone with their dependants (see Chapter 4).

### **Grooming partners**

Injured mothers have fewer high ranking adult males as grooming partners. Adult males spend much of their time in large mixed sex groups, and it is possible that injured mothers groom less with them as they spend less time in these types of groups. Some non-injured mothers (Kutu and Zimba) also had no adult males as grooming partners. For two of them individual life histories seem to be having an impact on their behaviour. Kutu is the most recent immigrant of the females in this study, and it is likely that this is the reason that almost all of her grooming time is directed towards her dependants rather than other community members, and why she has very few grooming partners. That immigrant females associate less with other group members, and spend more time grooming their infants, has also been suggested in a previous study (Nishida 1988). Zimba had only one adult female grooming partner throughout the study period. All her grooming bouts with other community members are with this one female, who is thought to be her adult daughter, Kewayia. It has been shown that the relationship between a mother and her adult daughter results in higher grooming frequencies and longer durations of grooming (Muroyama & Sugiyama 1994). It is possible that the



presence of an adult daughter takes away some of the need to look elsewhere for a grooming partner. Furthermore Zimba's daughter (Kewayaya) is injured, and it may be possible that she grooms her more because of this injury.

It is difficult to say conclusively how the number of grooming partners is affected by injury owing to the limited amount of data available on female grooming partners. Also there is a good deal of individual variation; some individuals characteristically have many grooming partners, others just a few. What can be suggested from these results is that injured females have less high-ranking adult male grooming partners, perhaps because they spend less time in association with them.

### **6.7.3 Other factors that affect grooming**

Other factors that may affect the level of grooming in chimpanzees were discussed in the beginning of this chapter. They are briefly commented on here:

- Age and sex differences are reduced in this study as all focal subjects were from the same age/sex category – adult females with dependants.
- A dominance hierarchy between females was difficult to determine in this study (see Appendix 2), and as seen in section 6.3 there is no consistent result to imply that dominance is having an affect on grooming, so it was not taken into account here.
- The association of individuals has been shown to affect grooming in that two individuals that associate more are more likely to groom each other (Boesch & Boesch-Achermann 2000). Association is seen to have an impact in this study, particularly on the number of adult male grooming partners for injured mothers.
- Oestrus in females could affect the level of grooming seen. During the study period only three of the focal subjects were in oestrus. One of the



three (Janie) was lactating at the time, having given birth just prior to the beginning of the study. She reached oestrus stage 1 on one occasion, which lasted three days; this is not considered to be a true oestrous period. A second mother (Kalema) was pregnant during this study period and gave birth on 22<sup>nd</sup> August 2000, three months after the completion of this study. She would have conceived around the end of January with her last regular cycle. Her oestrous swellings after this time were irregular, often did not reach full size and continued for many days, almost a month in one instance; this level of oestrus is not likely to affect grooming interactions. Pregnant female chimpanzees are known to show anogenital swellings, both in captivity and in the wild (Wallis & Goodall 1993). Of the 41 observation periods that were collected on Kalema, she was in full oestrus for five of them. Of these five, she was involved in grooming interactions with other community members on two occasions. For the observation periods when she was not in oestrus she was not observed in any grooming interactions with other community members. Kalema, who is injured, was groomed more during full oestrus and so it is possible that her low rate of grooming interactions would have been even lower, had she not been in oestrus during the study period. The third mother (Nambi) had regular cycles throughout the study period. Four of these cycles were recorded. Nambi is the alpha female (see Appendix 2), and so it is expected that males would be very interested in her when she is in full oestrus. Unexpectedly, Nambi was more likely to be involved in grooming interactions with other community members when not in oestrus, than when in any stage of oestrus during this study period. Nambi, who is not injured, has shown a slight decrease in her grooming behaviour when in oestrus, so it is possible that her higher rate of grooming interactions would have been higher, had she not been in oestrus during the study period. None of these results greatly affect the overall results discussed in this chapter.

- Individual differences may also affect grooming behaviour. For example Kutu shows the lowest level of social grooming with other community

members, and the reason may be that she is the most recent immigrant study female in the community (as described above). Personality differences among individual chimpanzees must play a role in the grooming behaviours seen in this chapter.

## **6.8 Conclusion**

What is conclusive in this chapter is that the grooming behaviour of adult female chimpanzees from the Sonso community is affected by their injury status. The physical difficulties inherent in grooming, and the balance required, seem to be the reason why injured mothers groom others less frequently, rather than any lack of tolerance shown by other community members. Choice of grooming partners for injured mothers seems to be limited by the fact that they spent more time in smaller groups. Mothers with injuries do not reduce the level of grooming given to their offspring, despite physical difficulties in doing so, but more data are required to determine whether juveniles with injured mothers groom them to a greater extent than juveniles with non-injured mothers. There may be long-term social repercussions, such as a lower reproductive rate for the mother, if she is indeed unable to groom other community members to the same extent as non-injured mothers, or has fewer adult male grooming partners because she associates less with them.

## Chapter Seven

### **The impact of injuries on free-living chimpanzees - types of locomotion used, time spent moving and use of arboreal space**

*Early in the morning, after spending a few hours grooming each other high in the canopy, Zana and her juvenile son, Zalu start moving across to an adjacent tree where many figs are ripe. They both head toward the extremity of the tree they are in. Zalu easily crosses from the tree into the outer branches of the adjoining fig. Zana, in contrast, reaches out to grasp overhanging branches from the fig tree and loses her balance. She quickly returns to a more stable location closer to the trunk of the tree. Because of snare injuries neither of Zana's hands are able to grasp vegetation effectively, and she uses the crook of her elbows, or her wrists to hook onto branches or vines. She attempts the crossing a second time, using as many branches as she can to stabilise herself, but once again she loses her balance and retreats. Each time she retreats she rests for a minute before attempting the crossing again. On the sixth attempt she manages to secure enough supports to make a successful crossing. She quickly scrambles to a position where the branches are thicker and she is more stable. After a few minutes rest she joins Zalu and begins feeding on the abundant Ficus sur. (Budongo Forest: March 2000)*

#### **7.1 Introduction**

Locomotion is a fundamental component of a chimpanzee's survival in the wild. Moving around in the canopy and on the ground is a skill much needed in the everyday life of chimpanzees in order to gain access to food and social partners, to assist young and to flee from potential danger. That so many chimpanzees in Uganda and elsewhere have survived disabling injury to one or more limbs suggests that they have learned to cope with their locomotor deficiencies.

This chapter will examine the extent to which an injured chimpanzee's locomotor behaviour is different from that of non-injured chimpanzee, and will discuss how



this may affect its ability to travel. If injured chimpanzees have difficulties with locomotion, and consequently spend less time travelling, this may in turn affect their grouping patterns and have negative social consequences. These may include fewer opportunities for social interactions, reduced opportunities to gain group knowledge such as feeding sites, and less protection from other group members. This chapter will also examine the degree to which injured individuals are able to access different areas of a tree. The extremities of a tree are often the areas where balance would be most essential, and because of this, injured chimpanzees may spend less time there. If injured females are found to spend a significantly larger proportion of time in any particular part of a tree, perhaps they have less choice about which part of the tree they can use, which would affect access to food and general movement as well as giving individuals less opportunity to initiate social contact.

## **7.2 Previous studies on the effect of injuries on types of locomotion, travelling and use of arboreal space in chimpanzees**

### **Effects of injuries on types of locomotion used**

Very little has been documented about the effects of disabilities on types of locomotion used in chimpanzees. Chapters One and Two cover the available literature on injuries to chimpanzees, both at the research site and from other locations throughout Africa. The studies where injury is recorded as having an effect on locomotion include the following:

- the anecdotal observations at Gombe National Park, when an outbreak of a paralytic disease, that was almost certainly poliomyelitis, left 12 individuals affected (Goodall 1968). Three died (two were killed for humane reasons as they were so badly affected), three disappeared, and six individuals were left crippled. The six were described as adapting well to their injuries; those with paralysed arms adapted by using bipedalism, successfully enough that after a few months they were able to keep up with other group members (Goodall 1968).

- a study on bonobos (*Pan paniscus*) at Wamba, DRC, reported changes in locomotion techniques for individuals that had physical abnormalities (Kano 1984). One particular male's locomotor activities were severely affected by his injuries. Since his legs were stiff, he used "crutching", a method whereby the legs are swung between the arms, and then the arms are swung forward again. Less disabled bonobos were quite agile and active both in the trees and on the ground, but noticeable differences such as lack of continuous arm swinging in individuals with injuries to the hands were observed (Kano 1984).
- a study, at Ngogo, Kibale National Park, described an injured female, with a stump as a right hand, as an "unbelievable daredevil" (Ghiglieri 1988, p.147). She is described leaping across empty space between neighbouring branches, rather than returning to the bole of the tree as most other chimpanzees did. Despite her injury she seemed both an excellent climber and an acrobatic one, although there is no mention of her behaviour prior to injury (Ghiglieri 1988). Other injured chimpanzees observed did not display such acrobatic abilities.
- a brief study on the effects of injury on the locomotion of the study community found that individuals with snare injuries to the forelimbs used modified, but very successful adaptations for arboreal locomotion. Those individuals with injuries to the hind limbs were more awkward and slow (Quiatt 1996).

### **Effects of injuries on travelling**

During his study at Ngogo, Ghiglieri spent time at the nearby site of Kanyawara, where he saw many more snare injured individuals than he had witnessed at Ngogo. He describes one particular day when two small groups split off from a large party of chimpanzees who were travelling a long distance to a food source. Although it is commonplace for chimpanzee parties to break into small groups, both these groups contained injured individuals, and it was thought they had broken away from the main travelling group as they could not keep up. One group included only two chimpanzees, both injured, and the second was a family group



(mother, infant, juvenile), of which the juvenile was injured (Ghiglieri 1988). Another example is of a chimpanzee at Gombe with a congenitally deformed foot. This chimpanzee was described as having difficulty keeping up with a travelling party of adults (Goodall 1986). Ghiglieri suggested that if chimpanzees with injuries are unable to remain with a travelling party, they become isolated not only from the protection of the larger group, but also from the social interactions that occur within that group (Ghiglieri 1988).

### **Effects of injuries on access to arboreal space**

A study focusing on the Sonso community examined how access to different parts of the tree is influenced by physical ability and/or social rank. Smith (1995) looked at the effects of limb injuries when chimpanzees were feeding on *Ficus sur*. His results implied that injured chimpanzees were less likely to feed on the large clumps of figs found at the trunk of the tree. This was argued to be because injured chimpanzees were physically unable to hold onto the large clumps of figs whilst feeding, or because injured chimpanzees had a lower dominance status which was likely to have affected their access to favoured food sources (Smith 1995).

### **7.3 Locomotion in able-bodied chimpanzees**

Chimpanzees in the wild spend around 14% (at Taï Forest) to 18% (at Gombe National Park) of their time in locomotor activities (Doran 1993). Chimpanzees travel both in the trees and on the ground. In a study conducted on the chimpanzees in Taï Forest, Ivory Coast, arboreal activities were found to account for 16% of all locomotor activities, and 84% were accounted for by terrestrial activities (Doran 1993). Long distances between feeding and resting sites are most frequently travelled along the ground using knuckle-walking quadrupedalism (Doran & Hunt 1994). There are differences between the sexes in the distance travelled between resting sites, feeding sites, and over the entire day range, with females travelling shorter distances than males (Wrangham & Smuts 1980).



Locomotion type varies depending on the substrate used. Chimpanzees are adapted to travel both on the forest floor and in the canopy, and the mode and pattern of locomotion differs depending on the substrate utilised.

When travelling along the ground chimpanzees use quadrupedalism, a method of locomotion that employs all four limbs in a definable gait (Doran 1993). One of the forms of quadrupedalism for which chimpanzees are best known is knuckle walking. This is when they are walking or galloping on four limbs and the backs of the middle phalanges of the flexed fingers are placed on the ground (Goodall 1968). The sequence of movements is that the left foot is placed laterally to the left hand and the right foot medially to the right hand, or the left foot medially to the left hand and the right foot laterally to the right hand (see illustration in Goodall, 1968: 178). When moving fast along the ground in a gallop the two hands are lifted from the ground, one slightly after the other, and as they touch the ground the two feet are lifted, once again one slightly after the other. When travelling down a steep slope a chimpanzee often uses its arms as crutches whilst swinging the legs through (Goodall 1968). Tripedalism is another form of terrestrial locomotion where one hand is used to carry an object. Bipedalism is a separate form of locomotion where the weight is borne on the hindlimbs and the trunk is vertical (Doran 1993). Bipedal locomotion is used occasionally, either when searching for another chimpanzee or when looking for something in the distance, when carrying food in the hands, when walking through long grass, or during aggressive displays.

Arboreal locomotion involves the use of palmigrade quadrupedalism, a further type of quadrupedalism where the hands grasp the substrate (Doran 1993). Knuckle walking is also seen in trees, but only when the branch is horizontal and sufficiently wide. Arboreal locomotion includes the use of climbing and scrambling when moving through the canopy and through areas that are thickly meshed with lianas and vines. Both hands and feet are used in varying combinations for methods such as vertical climbing, scrambling, crossing over between branches and foliage of adjacent trees, and tree swaying (used when the next tree is out of reach; body weight is used to sway the first tree until the next tree can be reached). Other methods used in the arboreal context include leaping

and diving, as well as suspensory behaviour (including arm swinging and dropping from a higher to a lower substrate) (Doran 1993). Chimpanzees are classed as 'modified brachiators', and only occasionally show the pure form of arm-swinging locomotion (Napier & Napier 1985). Vertical climbing is used when climbing up into a tree; usually the chimpanzee has its arms around the trunk, with the feet in the normal walking position; achieving movement by pushing legs and feet into the trunk, and reaching up the trunk with the hands. Climbing down a trunk can be achieved by simply sliding down, 'fireman's pole' style, or by slowly walking the arms and legs down in a similar posture to the one used when climbing up the trunk. Often chimpanzees avoid coming down thick trunks and use neighbouring branches to climb down (Goodall 1968).

Two populations of the eastern subspecies of chimpanzees (*Pan troglodytes schweinfurthii*) differed very little from each other in locomotor activities, despite differences in habitat (Doran & Hunt 1994). The major difference was that Gombe chimpanzees were more arboreal than Mahale chimpanzees. When these two populations were compared to a population of the western subspecies of chimpanzees (*Pan troglodytes verus*), there were differences in the types of locomotion used. Taï chimpanzees used more climbing and scrambling and less quadrupedalism than the two eastern populations. The Taï population were the only ones to show sex differences in arboreal locomotion, the adult males using less quadrupedalism, and more climbing, tree swaying and bipedalism than females (Doran & Hunt 1994). The three populations were similar in that they all travelled along the ground in between feeding and resting sites and used knuckle-walking quadrupedalism most frequently (Doran & Hunt 1994). Taï chimpanzees were more arboreal than either Mahale or Gombe chimpanzees, although females at all three sites were more arboreal than the males. Also, Taï chimpanzees spent greater amounts of time at heights greater than 20 metres than either of the two other populations. Once again there was a sex difference for Taï chimpanzees, with females spending more time in the trees as well as a greater proportion of time at above-ground heights, especially heights above 20 metres (Doran & Hunt 1994).

## **7.4 Aims of this chapter**

The aim of this chapter is to determine what forms of locomotion chimpanzees with injuries use, and if modified forms of locomotion are used, how does this affect the travelling behaviour of individuals? And if travelling behaviour is affected, how does this impact on other aspects such as social behaviour?

A further aim of this chapter is to determine whether injured individuals are using all parts of the tree to the same extent as non-injured chimpanzees. If they do not, how does this affect aspects such as social and feeding behaviour?

## **7.5 Methods**

### **Definition:**

Moving and travelling (refer to the same thing throughout): the transit from one feeding or resting location to another, whether it be to a neighbouring branch, an adjacent tree, or a site some distance away.

### **7.5.1 Time spent moving and descriptions of locomotion**

Focal animal sampling was used to determine the amount of time individuals spent travelling, and ad-lib sampling was used to describe the different methods of locomotion used by injured chimpanzees at Sonso. Mixed linear models were used for statistical analysis of time spent moving and time spent moving in arboreal space, following the outline described in Chapter Three. Factors included in the models were season (section 3.4.6) and severity of injury (section 3.3.3). The Bonferroni correction method for multiple comparisons is used (section 3.5.2) with a resulting significance level of 0.025. Time spent feeding (in relation to time spent arboreal) was calculated using focal animal sampling and analysed using mixed linear models.

Total time spent in arboreal space (regardless of behaviour) was calculated using scan sampling, with data collected at five-minute intervals. Four arboreal positions



were combined - position one, two and three, and in a sapling (section 7.5.2) and compared with the number of scans from when individuals were on the ground. Scans that were out of sight were not included. A binomial GLM was used to analyse the data (see Chapter 3) and included severity of injury (section 3.3.3) and the degree of habituation (see Table 7.1) as factors in the model.

Degree of habituation

Habituation levels affected the amount of time I was able to observe individuals moving (and resting) on the ground. In this study the level of habituation for the 12 females did differ, with some individuals being very relaxed in the company of researchers, and others very shy. Table 7.1 shows my judgment of the level of habituation for the study females to both myself, and my field assistant, over the study period. It must be noted that it is both difficult and subjective to determine levels of habituation. It is not clear-cut, and can change day to day – some females that normally are well habituated can on some days flee from observers. Habituation is also affected by the presence of other chimpanzees and also the number of researchers observing the group.

Table 7.1      Level of habituation of study individuals (injured individuals in bold)

Level of habituation			
1 – High (relaxed)	2	3	4 – Low (shy)
Nambi NB	Kwera KW	<b>Kigere KG</b>	<b>Zana ZA</b>
Zimba ZM	<b>Kalema KL</b>	Ruda RD	Ruhara RH
	<b>Kewayya KY</b>	<b>Banura BN</b>	Kutu KU
	Janie JN		

7.5.2    Use of arboreal space

Five-minute scan samples were taken in order to determine the use of arboreal space. A simple, relative measure was used to determine whether injured mothers

tend to use branches closer to the main trunk rather than going out to the extremities. This was measured using the radius from the main trunk out to the far extremities of the branches, and dividing this into three to determine the positions used to describe the different areas of arboreal space.

Codes and measures used for five-minute scans:

- P1 – position one, the third closest to the main trunk
- P2 – position two, the third in between
- P3 – position three, the third farthest from the main trunk
- OG – on the ground
- SAP – in a sapling (less than 40 cm d.b.h.)
- OS – out of sight

In order to analyse these results a binomial GLM was used to compare the proportion of time spent in each position. Factors included in the model were the injury status of the mother, the severity of injury of the mother, and whether the group was feeding or not feeding. Unfortunately, details of feeding behaviour (i.e. the particular food type) could not be included, as such data were recorded in the focal animal sampling rather than at the five-minute scans. The Bonferroni correction method was used with a resulting significance level of 0.017. Some results significant to the 0.05 level (but not to the 0.017 level) are included in order to express general trends seen in the data. In these cases exact p-values are given.

## **7.6 Results**

### **7.6.1 Types of locomotion used by injured chimpanzees of the Sonso community**

In general the injured chimpanzees of the Sonso community use modified forms of the patterns of locomotion described in section 7.3. For instance, chimpanzees with injuries to the hands can only use modified versions of knuckle walking. Some do not have knuckles, or the knuckles are mangled and distorted in such a fashion that it is difficult to place them at an angle where they will touch the

ground. Tripedal locomotion is very common for chimpanzees with injuries to one hand. The injured hand is held upwards towards the chest, while the other three limbs are used. Chimpanzees with fore-limb injuries are affected in different ways from chimpanzees with hind-limb injuries. Below are more detailed descriptions of the modified locomotion techniques used by the five injured chimpanzees in this study.

#### **Banura (congenital deformity – swollen left foot)**

On the ground Banura walks using quadrupedalism placing weight on her deformed foot as she moves. She mostly places weight on the tips of the deformed digits, rather than on the sole of her left foot. Less frequently she walks placing weight on the sole of her deformed foot. She has also been observed walking tripedally, holding her left foot off the ground. This has been observed very occasionally and always when she is trying to move quickly, for example when trying to cross either of the two main roads that dissect the forest, or when travelling alone. When observed from behind as she walks along a trail, Banura's hips tilt in order to compensate for both the awkwardness of her step and the different lengths of her legs.

When climbing and scrambling in arboreal space, Banura cannot use her injured foot as she cannot use it to cling or grasp. This foot is either used for balance, by placing it alongside a branch, or holding it outwards at varying angles. She cannot use her foot for vertical climbing, but when moving horizontally in arboreal space along wide branches she is able to use her foot as she does when moving on the ground.

#### **Kalema (snare injury – right hand)**

Kalema has been seen using both knuckle walking and tripedalism when travelling on the ground. She uses a modified version of knuckle walking: the right hand is placed with the back of the wrist touching the ground, rather than the back of the middle phalanges. Her left hand is used for knuckle walking in a way similar to able-bodied chimpanzees. When arboreal she has been observed to use



tripedal locomotion when moving along a thick branch that is parallel to the ground.

When vertical climbing up or down the trunk of a tree, Kalema uses her injured hand, which has no ability to clasp, for balance by holding it out at varying angles. She often uses the back or side of her hand for balance by placing it against the trunk of a tree or branch. She also uses the crook of her right elbow, or her right hand hooked over a branch, when climbing down for balance or to help pull her up.

When climbing and scrambling she uses her right arm only for balance by holding it out in different directions or by pushing it against a substrate. She is unable to use arm swinging as she cannot grasp with her right hand.

#### **Zana (snare injuries – both hands)**

When terrestrial, Zana walks quadrupedally. As both hands are deformed, she uses the back of her left wrist as the point of contact with the ground in a modified form of knuckle walking. The fingers of the left hand are splayed out to the side. It appears that she also uses the back of her right wrist for a modified form of knuckle walking, although it was difficult to observe. I followed Zana along a forest trail for 15 minutes and during this time she had little obvious difficulty with this form of locomotion; although very few times in the ten months of observation did I see Zana travelling along the ground, and I never saw her moving quickly. The two times that she was directly observed travelling with the group, she was last to leave the food source and ended up travelling alone, meeting up with the group at a later time. More commonly Zana would remain at a food source long after the main group had left, often spending the rest of that day in the tree with her juvenile son.

Zana moves very slowly and deliberately in the trees. Many times I have seen her hesitate when crossing from the extremity of one tree to the next (bridging and tree swaying); on one occasion she hesitated five times before making it across on the sixth attempt (see description at beginning of this chapter). I have never seen

her involved in any suspensory behaviour and believe these forms of locomotion would be impossible for her. I have observed her walking tripedal along thicker branches, holding her left hand up. When climbing and scrambling in arboreal space she uses the back of her left hand against branches to help with balance. She also uses her forearms and elbows to assist by leaning against them or using them to pull herself up.

#### **Kewayaya (snare injury – right hand)**

When terrestrial, Kewayaya uses quadrupedalism. She uses a modified version of knuckle walking on the right side, using the point just above the right wrist as the contact point with the ground, with her fingers splayed out to the side. Her left hand is used similar to able-bodied chimpanzees.

When vertically climbing, Kewayaya uses the back of her injured hand, placed against the trunk, to help her balance when climbing both up and down. When climbing and scrambling she holds her injured hand out at an angle to help with her balance. She also uses her injured hand as a hook to support herself. She is unable to use continuous arm swinging as she cannot grasp with her right hand.

#### **Kigere (snare injury – right foot missing)**

When moving on the ground Kigere knuckle walks, using her stump as a foot. She appears to place even weight on both sides, and as a consequence her hips tilt considerably as she walks, compensating for the shortness of her injured leg. Once I observed her running tripedally on the ground, holding her right foot above the ground by tucking her right knee up to her chest. On this occasion she was alone and moving quickly in order to try to catch up with a group of chimpanzees that were travelling further along the trail.

When moving in trees she uses her stump during quadrupedalism (as when terrestrial), or for balance (by lightly touching against branches), or holds it out of the way. Twice, when arboreal, Kigere was observed to be off balance. For example, on one occasion she was trying to reach a favourite feeding position by

bridging from one tree to the next, but she lost her balance and had to return to her original position in order to stabilize herself before attempting to cross again. It would seem that this kind of behaviour is potentially fatal for a chimpanzee.

Despite using modified forms of locomotion, inventing new methods to assist in locomotion and avoiding some locomotor types, all five injured chimpanzees have been observed using both arboreal and terrestrial locomotion. These modified forms of locomotion have been seen to affect the balance needed for arboreal travel in some individuals, as well it may affect the speed at which they can travel, especially when moving quickly on the ground.

#### **7.6.2 Time spent moving**

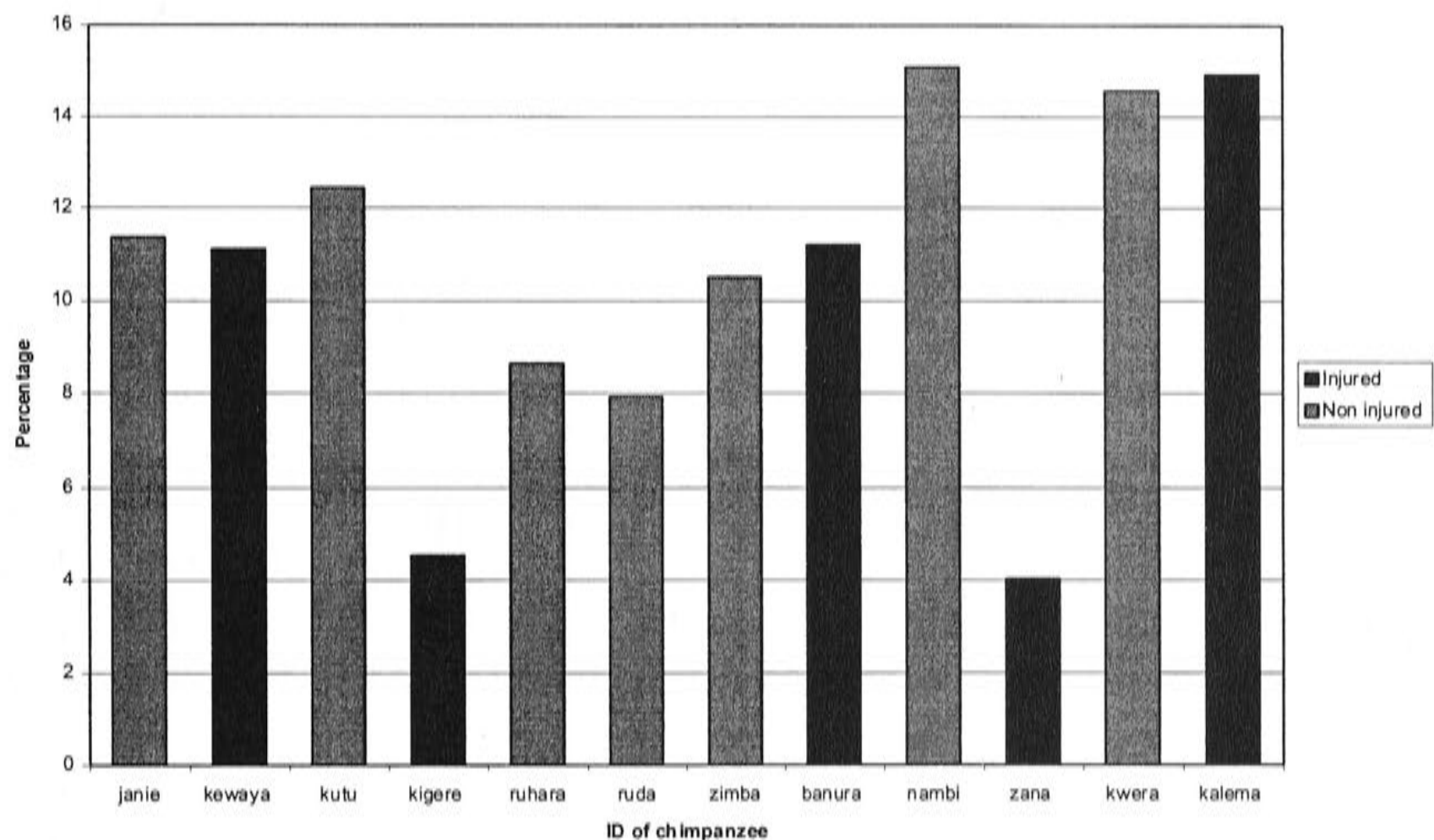
On average adult females in this study spent 10.5% of their time in locomotor activities. The percentage of total time that each focal subject spent in locomotion is plotted on the histogram in Figure 7.1. As with other figures, the females are ordered from left to right along the base of the graph, with the female with the youngest dependant on the left through to the female with the oldest dependant on the right. Two injured individuals, Zana and Kigere, spent around 4% of their time in locomotion whereas all other individuals spent 8% or more (up to 15%) of their time in locomotion. Interestingly Zana and Kigere are classed as the most severely injured individuals in this study (section 3.3.3).

A linear mixed model revealed that both severity of injury (Wald statistic=18.81, d.f.=2,  $p<0.001$ ) and season (Wald statistic=16.90, d.f.=1,  $p<0.001$ ) significantly affected the time spent moving. The most severely injured individuals spent a significantly lower proportion of time moving than either less injured or non-injured individuals. There was also a season effect, in that both injured and non-injured chimpanzees moved proportionally less in the wet season, and more in the dry season. This may be influenced by a possible shortage of food in the drier months, so chimpanzees had to travel more extensively to locate food sources. Data were collected for eight months in this study, so all seasonal differences are



based only on the months that were studied, and do not span an entire year (section 3.4.6).

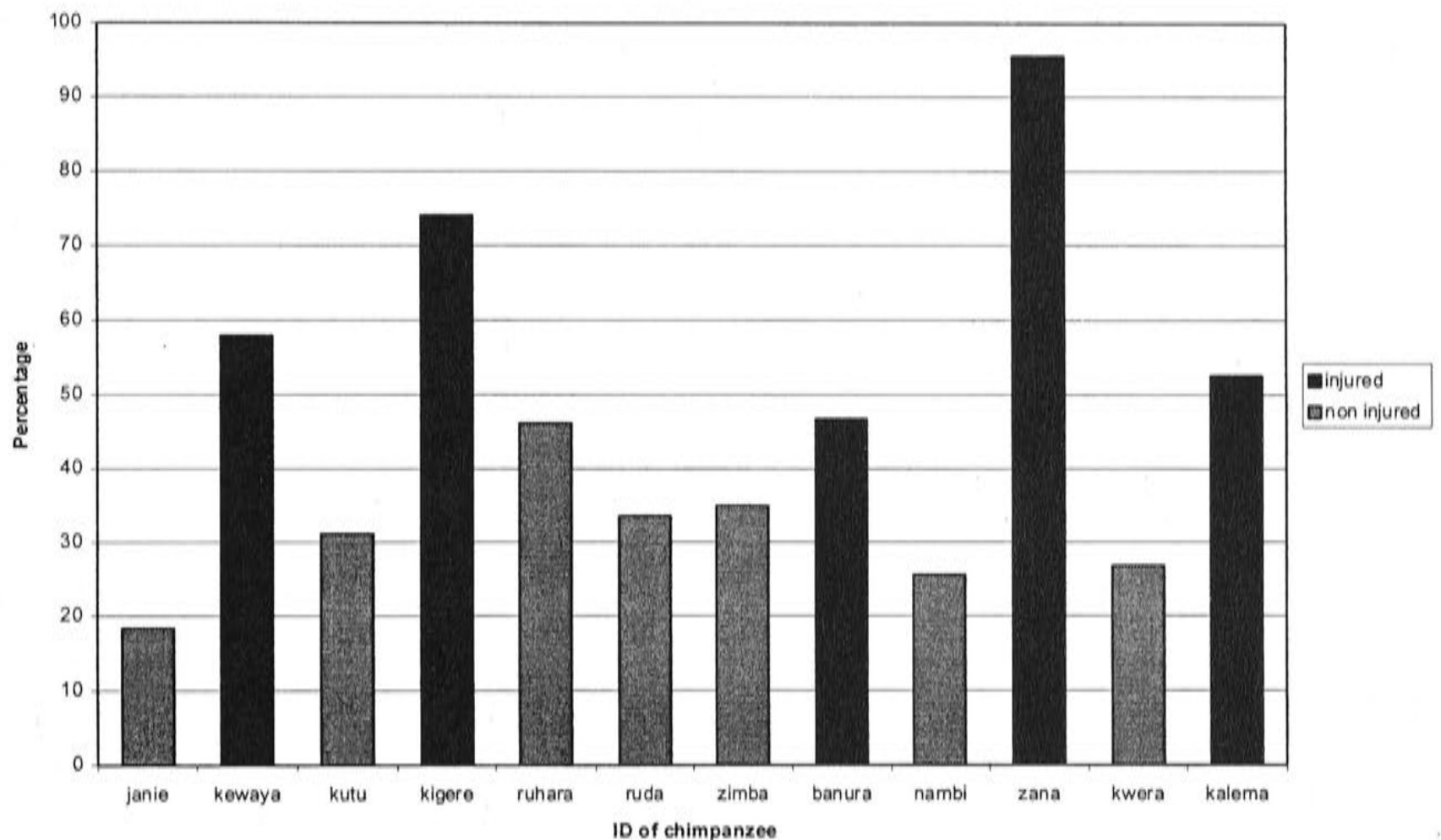
**Figure 7.1** Travel time as a percentage of total observation time (refer to Table 3.6 for number of observation periods and total time observed)



In order to determine the differences between travel time in the trees and on the ground, the total time spent moving was broken down into time spent moving in arboreal and terrestrial space. All of the injured chimpanzees spent more time moving in arboreal space, as a percentage of the total time spent moving, than non-injured chimpanzees (see Figure 7.2).

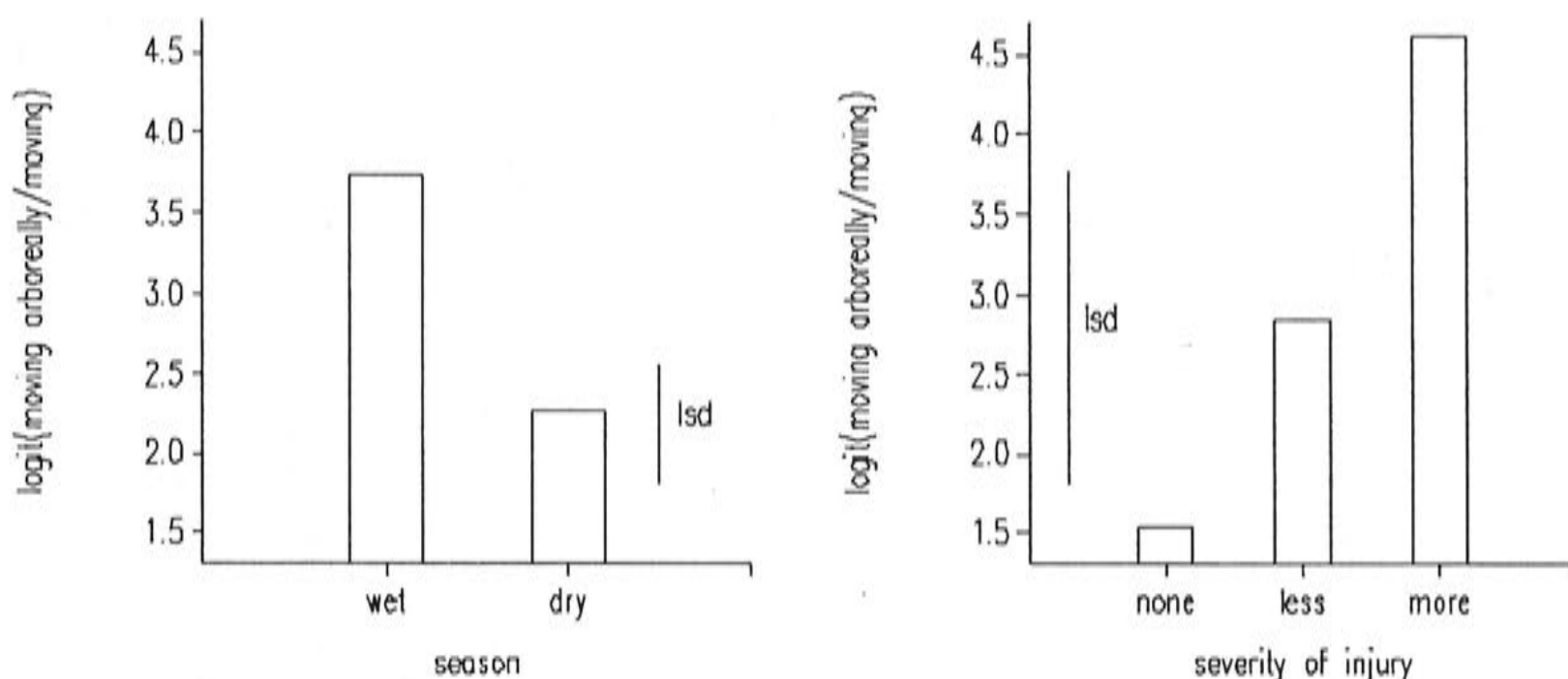
A linear mixed model revealed that both severity of injury (Wald statistic=10.58, d.f.=2,  $p=0.005$ ) and season (Wald statistic=17.31, d.f.=1,  $p<0.001$ ) significantly affected the time spent in arboreal locomotion. The greater the severity of injury the larger the proportion of travelling time was spent in arboreal locomotion. Less injured chimpanzees spent a significantly greater proportion of their travelling time in arboreal locomotion than non-injured chimpanzees, and the most injured chimpanzees spent more than either less injured or non-injured (see Figure 7.3).

**Figure 7.2** Time spent in arboreal locomotion as a percentage of total time in locomotion  
(refer to Table 3.6 for number of observation periods and total time observed)



Season affected the time spent travelling arboreally, both injured and non-injured individuals spending more time moving in the trees in the wet season than in the dry (see Figure 7.3). As food was generally harder to find in the dry season, chimpanzees spent a lot of time on the ground travelling between food patches, or searching for food. A high number of *Cyanometra* seeds were eaten off the forest floor in the dry season. *Cyanometra* pods burst in the heat of the dry season, scattering hundreds of seeds to the ground. The time spent searching for *Cyanometra* seeds was recorded as feeding, not moving, although the presence of these seeds meant that chimpanzees spent more time on the ground. In the wet season, when many figs were fruiting, chimpanzees spent more time in the trees travelling from one part of the tree to the next.

**Figure 7.3** Time spent moving arboreal as a proportion of the total time spent moving



The above results suggest that when moving, injured chimpanzees move proportionally more in trees and proportionally less on the ground than non-injured chimpanzees. In order to interpret these results it is useful to know whether injured chimpanzees spend more time in trees overall, regardless of activity, than non-injured chimpanzees.

Figure 7.4 shows the percentage of 5-minute scans that each individual was found on the ground and in the trees. The remainder of time not included on the graph represents time out of sight. Both Figure 7.4 and 7.6 show non-injured females grouped on the left of the graph and injured females grouped on the right; they are not in order of age of infant as for previous figures (this is because more than one factor needed to be presented).

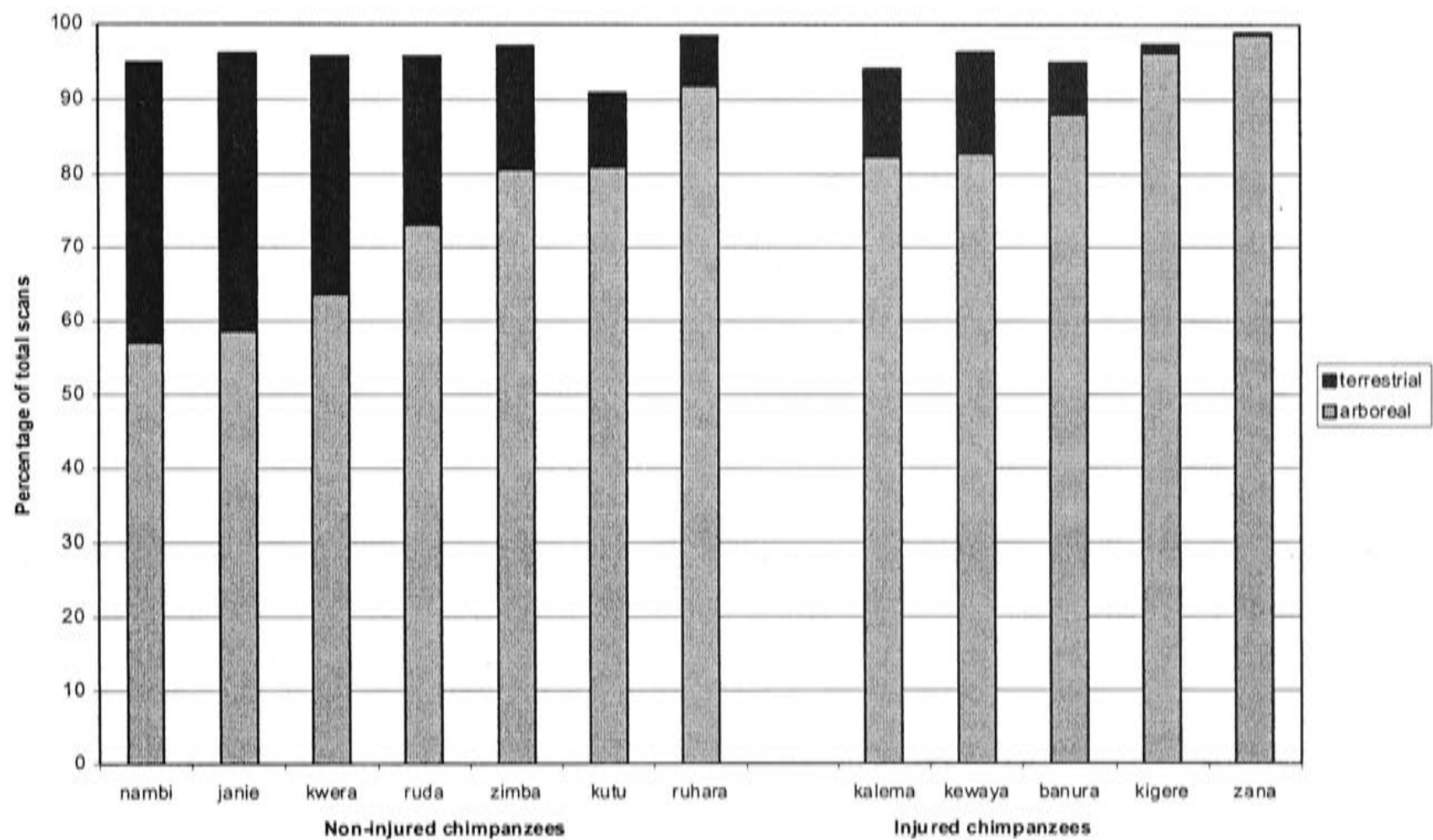
It appears from Figure 7.4 that injured chimpanzees spent more time in arboreal space than non-injured chimpanzees, although there is some overlap (Zimba, Kutu, Ruhara). Kigere and Zana once again show the most distinct result, spending almost all of their time in the trees, and the least time on the ground.

A binomial GLM revealed that both the severity of injury ( $F=26.80$ ,  $d.f.=2,422$ ,  $p<0.001$ ) and the degree of habituation ( $F=8.92$ ,  $d.f.=3,422$ ,  $p<0.001$ ) significantly

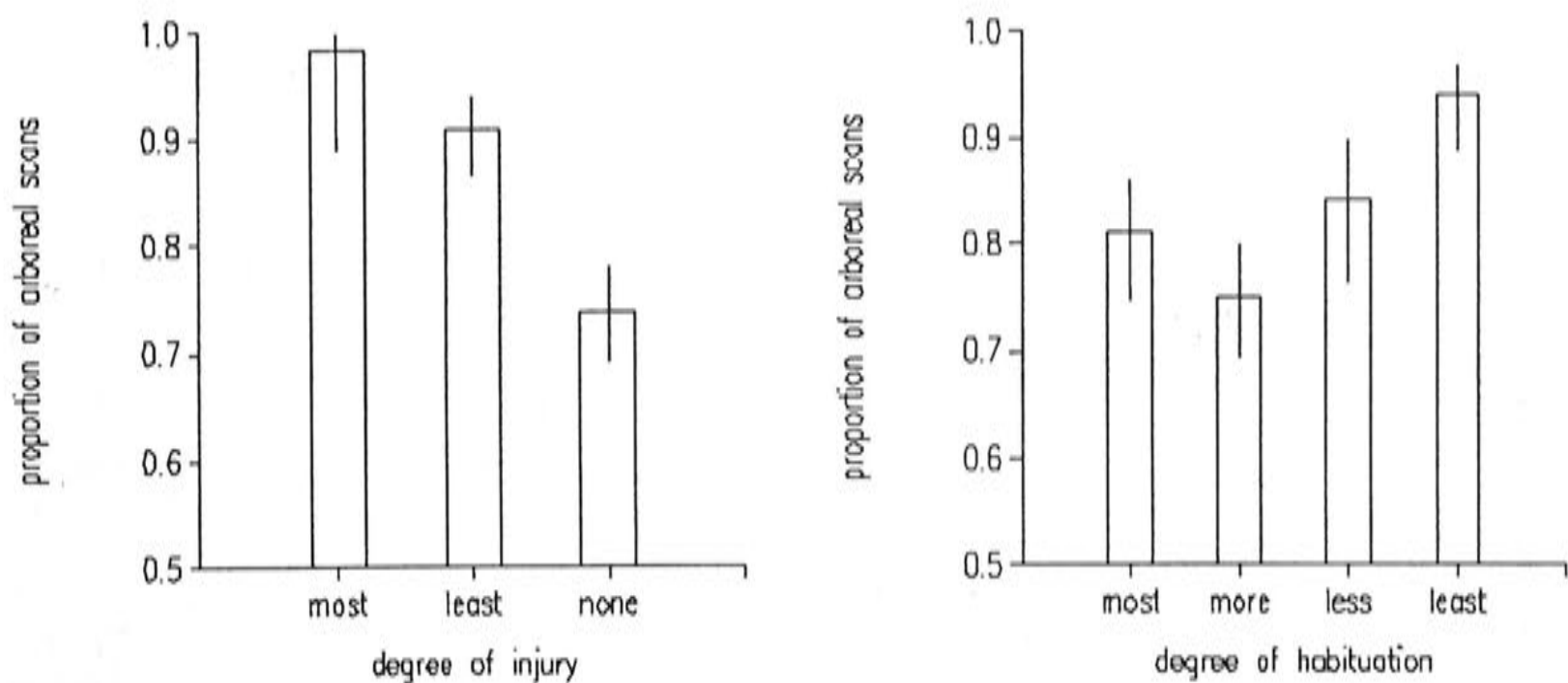


affected the proportion of scans spent arboreal or terrestrial (see Figure 7.5). The more severely injured individuals, and the least habituated individuals spent the greatest proportion of scans arboreal. This means that severely injured chimpanzees with low habituation are spending the most time arboreal, and non-

**Figure 7.4** Percentage of 5-minute scans that individual was arboreal or terrestrial (refer to Table 5.2 for number of scans used in analysis)



**Figure 7.5** The proportion of scans spent arboreal with the effects of both severity of injury and habituation



injured chimpanzees with a higher level of habituation are spending the least amount of time in arboreal space.

### **7.6.3 Use of arboreal space**

Ad-lib data from observations of both Zana and Kigere, the two most severely injured in this study, revealed that they both had difficulties when moving in the extremities of some trees, especially when trying to cross from the extremity of one tree to the next.

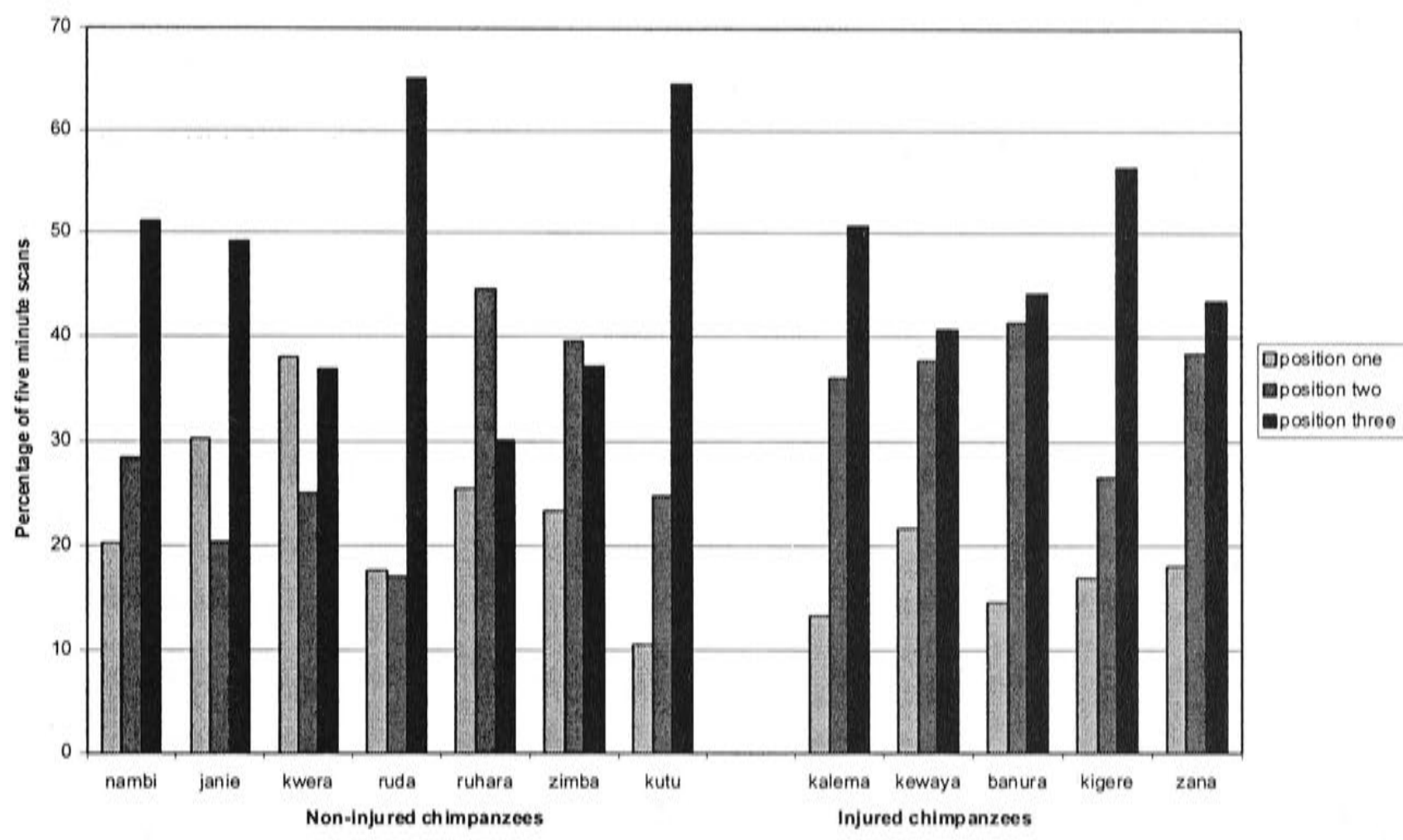
Time spent in different parts of the tree was analysed to determine whether injured chimpanzees are using all parts of the tree to the same extent as non-injured chimpanzees. Percentages of scans were calculated for all individuals at each of the three positions (position one: the third closest to the main trunk, position two: the third in between, and position three: the third farthest from the main trunk); this is summarised in Figure 7.6.

Figure 7.6 shows no obvious trends with respect to injury status, but there does appear to be a common trend for all individuals to spend a greater proportion of scans in position three, furthest from the main trunk.

A binomial GLM revealed no significant differences for time spent in position one, but a trend could be seen where both injury ( $F=4.09$ , d.f.=1,359,  $p=0.04$ ) and the combined effect of injury and feeding behaviour ( $F=3.89$ , d.f.=1,359,  $p=0.05$ ) affected the proportion of scans individuals spent in position one. Non-injured chimpanzees spent a greater proportion of scans in position one than injured chimpanzees, and injured chimpanzees spent less time in position one when not feeding than non-injured chimpanzees.

A binomial GLM revealed that injury had no effect on the number of scans spent in position two ( $F=2.33$ , d.f.=1,357, n.s.).

**Figure 7.6** Percent of five minute scans when focal was in trees, that focal spent in each of the three positions  
(refer to Table 5.2 for number of scans used in analysis)



A binomial GLM revealed a non-significant trend showing that the combined effect of injury and feeding activity affected the time spent in position three ( $F=5.09$ ,  $d.f.=1,359$ ,  $p=0.025$ ). Non-injured chimpanzees spent a greater proportion of scans in position three when feeding than injured chimpanzees, and a lower proportion of scans in position three when not feeding than injured chimpanzees. Injured chimpanzees spent around the same amount of time in position three regardless of whether they were feeding or not.

### 7.6.4 Time spent feeding

Since feeding is primarily an arboreal activity for chimpanzees at Budongo it was necessary to determine if injured chimpanzees spent more time feeding than non-injured, which may affect the time spent arboreal. A binomial GLM found no significant difference between the time injured and non-injured chimpanzees spent feeding ( $F=1.54$ ,  $d.f.=1,449$ ,  $n.s.$ ).



### **7.6.5 Summary of Results**

1. Chimpanzees with injuries use modified forms of locomotion, avoid some forms of locomotion altogether, and also use some similar methods to able-bodied chimpanzees, depending on the nature and extent of their injury.
2. Chimpanzees with the most severe injuries spent significantly less time moving than both less injured and non-injured chimpanzees.
3. Injured chimpanzees spent significantly more of their travelling time in arboreal locomotion than non-injured chimpanzees. The greater the severity of injury the larger the proportion of travelling time was spent in arboreal locomotion.
4. Chimpanzees with injuries spent less overall time on the ground than non-injured chimpanzees.
5. A trend was seen with both injury and feeding behaviour affecting the proportion of time spent in positions one and three.
6. No difference was found for injured and non-injured in time spent feeding.

## **7.7 Discussion**

### **7.7.1 Methods of locomotion used by injured chimpanzees of the Sonso community**

Injured adult female chimpanzees at Sonso use many modified forms of locomotion, as well as using unique methods to assist in locomotion. The character of an injury determines the type of accommodation adopted, and the number of injuries also affects the level of locomotor disability. As many of these chimpanzees have had their injuries for more than ten years prior to this study (since before the Budongo project began), these methods of locomotion must be adequate for their survival. That injured chimpanzees can move adequately is also reported in the studies described earlier in this chapter (Ghiglieri 1988; Kano 1984). Although injured chimpanzees can adapt their locomotion, the results suggest that injured chimpanzees do have difficulties with some forms of

locomotion, and generally, injured individuals are more cumbersome in their locomotion.

### **Arboreal**

When watching even the most injured individuals make their way up to the top of a giant rainforest tree, the casual observer is likely to conclude that chimpanzees who survive their injuries, and any subsequent infection, can learn to cope adequately with their disability. Only after watching these individuals for the length of this study period did I witness events such as Kigere losing balance and Zana struggling with bridging and tree swaying. These two individuals are the most severely injured, and seem to be at the greatest risk of losing balance and falling. The result could have serious repercussions for the individual, her dependant offspring and her community.

### **Terrestrial**

Although all five injured individuals were observed travelling on the ground with a reasonable level of ease, they travel more awkwardly, and perhaps more slowly, than non-injured individuals. Kigere and Banura, both with injuries to their feet, seemed to be the most disadvantaged on the ground because of the unbalanced nature of their movement. This was most obvious when they were trying to move quickly. Only once did I clearly see Zana move on the ground, and I never saw her attempting to move quickly. I believe that Zana, with two injured hands, would have had a lot of difficulty moving quickly on the ground. Kigere and Zana show a preference for arboreal resting. For example, on one particular occasion a group, of whom only Kigere was injured, were travelling along the ground between resting spots. Each time they stopped to rest, Kigere climbed up into a sapling rather than remaining on the ground to rest with the others. Zana also showed a preference for resting in arboreal space, and was observed only once resting on the ground in the eight months of the study. Injured individuals seem to show a preference for arboreal space.



### 7.7.2 Time spent moving and preference for arboreal space

Adult female chimpanzees at Sonso spent, on average, less recorded time in locomotion than has been recorded at other field sites (Doran 1993). It is, however, difficult to compare these data as the records from other field sites include both males and females, and females are known to travel less than males (Wrangham & Smuts 1980). Furthermore, females are less habituated than males in the Sonso community, so it is likely that this also affected the proportion of time that they were seen on the ground.

The two females with the most severe injuries (Zana and Kigere) spent significantly less time moving than all other females in this study. On many occasions they were seen feeding by themselves for extended periods of time; either they had remained in the feeding tree after other group members moved off, or they were encountered alone. They may have been behaving in this way to avoid long-distance travel on the ground because of their more cumbersome locomotion, or it may be that they were reducing feeding competition by exploiting only a few favoured feed sites. Reducing feeding competition by foraging alone has been discussed elsewhere as a strategy used by female chimpanzees to increase food intake (Wrangham & Smuts 1980). Either way, injury could be playing a very significant role.

Injured chimpanzees spent a significantly larger proportion of their travelling time in arboreal locomotion. Perhaps this is simply because they spent more time in the trees anyway. The question then seems: why do they spend more time in arboreal space? They may be doing this for the same reason why severely injured chimpanzees spent less time moving, namely that they may be more likely to stay at an arboreal feeding site after other group members have travelled onwards. As they stay up in the trees, rather than climbing down and moving to a different site, this increases the time spent arboreal. This was obvious for the more severely injured chimpanzees, but not so obvious for the less injured chimpanzees.

It is possible that there are other reasons why injured chimpanzees spent more time arboreal, and when travelling spent a greater proportion of that time moving



in the trees. They may choose to move between feeding and resting sites in the trees, rather than come to the ground (although this was rarely observed for long distances). Perhaps they are more likely to visit food sites that are at shorter distances, because it would be easier to travel through the trees to get to them. It may also be because they feel more vulnerable on the ground. The threat from predators and the avoidance of snares (which are all set at ground level) are two reasons why the ground could be perceived as more dangerous for injured individuals and thus avoided. Level of habituation of individuals and time spent feeding may also be factors influencing the time spent arboreal.

### **Chimpanzees 'safer' in the trees?**

#### **Reaction to ground predators**

Whether arboreal space is 'safer' than terrestrial is difficult to determine. Predators of chimpanzees include leopards (Boesch 1991; Hiraiwa-Hasegawa et al. 1986), lions (Tsukahara 1993) and humans. There are numerous reports of chimpanzees encountering or attacking leopards, leopards attacking chimpanzees, and predation on chimpanzees by leopards (Boesch 1991; Hiraiwa-Hasegawa et al. 1986; Poppenwimer 1999-2000; Tsukahara 1993). Lions have also been observed to kill chimpanzees (Tsukahara 1993). In many primate habitats predation risk from terrestrial canids, felids and snakes decreases as height above the ground increases (Boinski et al. 2000). Raptors are not reported to be major predators of chimpanzees (Treves 1999).

Studies on leopard and lion predation on chimpanzees note that one of the most common reactions of chimpanzees to feline predators was to climb up into a tree. For example Kortland used a dummy of a leopard and recorded the responses of chimpanzees, which included loud calling, screaming, climbing up a tree, intimidations and keeping silent (Hiraiwa-Hasegawa et al. 1986). In another study an encounter between a real leopard and chimpanzees was observed in which the chimpanzees' response was to emit loud alarm calls and climb high into the trees (Tutin & Fernandez 1991). A further study recorded alarm calls, whimpers, climbing into trees, and silence as responses from chimpanzees to the presence of

lions (Tsukahara 1993). It was suggested that climbing into trees was the most effective response. It was also suggested that females might be more vulnerable to attack by predators, as their habits are more solitary (Tsukahara 1993). These reports all support the idea that chimpanzees are safer from predators in the trees than on the ground.

No attacks by large carnivores on chimpanzees have been recorded for the Sonso community, and a recent survey of large mammals across the Budongo Forest found no evidence of large carnivore dung (Plumptre et al. 2001), suggesting that these species are now rare. Historically leopards were found in the Budongo Forest, and it is possible that some still exist, although they have not been sighted near Sonso for many years. In an early study at Busingiro, two sightings of leopard were recorded over a period of eight months (Reynolds 1965). Busingiro is to the west of Sonso, in the Budongo Forest Reserve; there is thought to be only one other community of chimpanzees between the Sonso and Busingiro communities (Newton-Fisher 1997). Lions are known to occur in the far northeast of the reserve at Kanyo-Pabidi, the site of one of the two tourist facilities within the Budongo Forest Reserve, and a leopard has been recently sighted in the forest just north of Kanyo-Pabidi (J. Donne, pers. comm.). Lions have been heard from the Sonso campsite on one known occasion in 1992, although it was an extreme dry season and it was thought that the lions might have been looking for water (A.Plumptre, pers.comm.).

Although there are apparently very few feline predators in the area surrounding the Sonso community, it is possible that chimpanzees still respond to the potential risk of an attack by a predator. Dunbar (1988) commented that mortality due to predation can sometimes be low or negligible in primates, and therefore it might be thought that it has little effect on social systems and group behaviour. He argued that it is not the actual mortality rate that is important, rather it is the potential risk of encountering a predator that may be important in affecting the behaviour of the prey species (Dunbar 1988). It is then possible that injured chimpanzees in this study are responding to a potential risk of predation. This may be especially so since it appears that injured chimpanzees are more vulnerable to

predation owing to their more cumbersome locomotion and their difficulty moving quickly.

Male chimpanzees nest lower than female chimpanzees at Budongo. One possible explanation is that males strategically locate their nests so as to protect the females and young from ground predators (Brownlow et al. 2001). This would support Dunbar's (1988) claim, and suggest that despite low predation pressure at Budongo, chimpanzees are acting primarily on the potential risk of predators.

It is not unreasonable to suggest that chimpanzees alter their behaviour because of a risk of predation. At Taï Forest, chimpanzees forage in relatively small parties. This is apparently a response to predation, as the chimpanzees live in a low visibility environment where reduced noise from small groups is more important than enhanced predator detection when groups are larger (Boesch 1991). Furthermore, Taï chimpanzees are found more frequently in all-male parties when an increase in predation pressure is recorded (Boesch 1991).

Even though predation pressure is currently low at Sonso, it is possible that this was not always the case, and perhaps chimpanzees still act in ways that previous generations did. Although a recent study of Diana monkeys, *Cercopithecus diana*, shows that changes in predation pressure affect prey behaviour even in the lifespan of an individual (Bshary 2001). When poachers imitated predator calls, monkeys in areas frequently poached were rarely fooled, but monkeys in areas that had recently been protected from poachers were deceived easily. So perhaps chimpanzees too learn to respond differently as predation pressure decreases over time. On the other hand, as will be discussed below, a prey's response to a human predator is different from its response to a feline predator. Changes in predation pressure recorded for human predators (e.g. as for Diana monkeys) may not necessarily occur when the predator is feline.

A further possibility is that females may have transferred from areas closer to areas where lions or leopards occur. They then would perhaps act in ways that reduce the threat from ground predators.



For one or more of the above reasons it is possible that chimpanzees respond to the risk of predation despite negligible predation risk, and that injured chimpanzees are more vulnerable to predation and so they avoid time on the ground where possible.

### **Avoidance of snares**

Another factor that could be responsible for injured chimpanzees spending less time on the ground, and proportionally less time moving on the ground, is that they are avoiding snares. Injured chimpanzees may relate spending time on the ground with the painful experience of becoming trapped, and possibly avoid ground travel where possible for this reason. People with their wire snares and traps can be seen as yet another type of ground predator.

### **Reaction to human threats**

Many cases already discussed show that a chimpanzee's response to threat is to climb up into trees (Hiraiwa-Hasegawa et al. 1986; Tsukahara 1993). In contrast I witnessed a number of occasions when chimpanzees fled on the ground after hearing a noise, or after the sudden arrival of researchers. Tutin and Fernandez (1991), in a study on the responses of wild chimpanzees to the arrival of primatologists, found that rapid jumping or sliding out of a tree or running at speed along the ground accounted for 59% of retreats, and slow and cautious almost silent descent from the tree and avoidance accounted for 16%. Climbing trees or escaping arboreally was not even mentioned in the list of responses. The same study reported chimpanzees calling and climbing into trees when they saw a leopard (Tutin & Fernandez 1991). This would seem to suggest that chimpanzees escape from human disturbance on the ground rather than in trees. An explanation may be that it would be impossible for a chimpanzee to outrun a leopard or lion on the ground, whereas it would be reasonably easy to outrun a human, especially in thick undergrowth. If so, humans are treated in a different way from other potential predators, and depending on hunting levels, humans may or may not be perceived as predators by chimpanzees.

### **Level of habituation**

As described in section 7.5.1 assessing the level of habituation for the study females was subjective. Despite this, the habituation scale in Figure 7.1 does suggest that there are differences in habituation, most obviously between individuals such as Nambi and Zimba (older and more dominant females who were confident around observers) and say Zana, Kutu and Ruhara (who were shy to observers). For most cases the chimpanzees in this study group did not flee from observers when seen (as described above by Tutin and Fernandez 1991), except in some cases when they were discovered travelling alone, or if observers arrived without being heard by the group.

When these habituation levels were used in the analysis (section 7.6.2) it was found that the least habituated females spent the most time arboreal. This indicates that less habituated females, who are shy to observers, may be more difficult to observe on the ground, or they may spend more time in the trees when observers are nearby. This suggests that habituation is a factor that affects the amount of time chimpanzees may be observed to spend on the ground, or in the trees. It also suggests that chimpanzees that are becoming habituated may not flee observers on the ground, as described above, but may spend more time in the trees where they feel safer.

Injury status of the study females was also found to be a factor affecting the time spent arboreal (see Figure 7.5). The most injured females behaved in the same way as the least habituated females, suggesting that either injury reduces the level of habituation or that both injured females and low habituated females prefer to spend more time in the trees, perhaps because they feel less threatened in arboreal space.

### **Time spent feeding**

The majority of food items in the diet of the Sonso chimpanzees are found in arboreal space (Stokes 1999), so an increase in time spent feeding may be the reason why injured chimpanzees spend more time arboreal. In a study that

compared the locomotor behaviour of several chimpanzee populations, Doran and Hunt (1994) found that some populations used arboreal space differently. When the chimpanzees from Mahale and Gombe were compared, it was found that Gombe chimpanzees spent more time in arboreal space. Gombe chimpanzees also spent more time feeding and, since feeding is primarily an arboreal activity, this accounted for the increased time spent arboreal (Doran & Hunt 1994). This was not the case in the present study as no significant difference was found when time spent feeding was compared for injured and non-injured females. Also in results relating to feeding efficiency from Stokes' (1999) study of the Sonso community, feeding efficiency was reduced only for some injured individuals, and not for all food types. Therefore it is unlikely that injured chimpanzees spent more time in arboreal space because they spent more time feeding.

### **7.7.3 Use of arboreal space**

The purpose of this part of the analysis was to determine if injured chimpanzees used all parts of a tree to the same extent as non-injured chimpanzees. All chimpanzees studied spent time in each position of the tree regardless of their injury. There was a trend showing that injured chimpanzees spent less time in the position closest to the trunk of the tree (position one). There was also a trend for position three, but this affected mostly non-injured chimpanzees, and there was no difference for position two. As the results showed only weak differences, it suggests that females in this study have access to all parts of the tree, to the same extent as non-injured, which allows them access to other individuals and food sources regardless of their injury status.

## **7.8 Conclusion**

Despite having adequate locomotor skills for survival, injured chimpanzees still behave differently from non-injured chimpanzees. That severely injured chimpanzees spent less time moving means that either their cumbersome locomotion affects their travelling behaviour, or they are reducing feeding competition, and so they may choose to remain at feed sites rather than move on with a large travelling party. This is supported by data in Chapter Four, which



show that injured chimpanzees spent more time alone, or in small groups. This then has social implications for these individuals, as they are isolating themselves from social opportunities that are important for their reproduction and survival. In section 7.2 a description was given of two small groups containing injured individuals in Kibale, breaking off from a large travelling group. This was thought to be because the injured individuals could not keep up, and it was argued that it led to serious social repercussions (Ghiglieri 1988). These results support Ghiglieri's ideas.

What is also conclusive from this chapter is that injured chimpanzees spent more time than non-injured chimpanzees in the trees, and more time moving in arboreal space. Many combining factors seem to be influencing this result including: difficulties in ground travel, so a preference for remaining arboreal at a feed site when the remaining group moves off; spending more time at one arboreal food source in order to reduce feeding competition; or spending time arboreal as injured chimpanzees may feel a greater threat from predators or snares when on the ground.

As discussed previously, the nature and severity of the injury are important factors when considering the effects of injury on locomotion. Level of disability appears to increase with the severity and number of injuries. As snaring is still a common problem in Ugandan forests, chimpanzees are at risk of receiving further injuries, and placing themselves at even greater disability.

## **Chapter Eight**

### **Discussion and Conclusions**

This thesis provides an analysis into the effects that limb injuries have on the behaviour of adult female chimpanzees from the Sonso community, Budongo Forest, Uganda. The results from this thesis can be used to help determine the level of threat that snaring places on chimpanzee populations. Both the results from this study, and the implications for the conservation of an endangered species, will be discussed in this chapter.

#### **8.1 Summary of findings**

Injured females with dependants, from the Sonso community of chimpanzees, behaved differently from those that were not injured. Four major behavioural parameters have been examined in this thesis, and each one has revealed, at least for some associated behaviours, that chimpanzees are affected by injury. The major results from each chapter are summarised below:

#### **Chapter 4 - Social grouping**

Chimpanzees have a fission-fusion social organisation that allows for groups of different sizes and compositions to be formed. Injured females were more likely to form smaller groups and spend time in family units than non-injured females. However, they did not show any preference for associating with either injured or non-injured adult females. Data on Social Time Index suggest that injured females may not be as well integrated into the community as non-injured females, although results were affected by the reduction in time that injured females spent in larger mixed-sex groups where opportunities for association were at their greatest.

## **Chapter 5 - Maternal behaviour**

A reduction in maternal behaviour has serious implications for young chimpanzees that are born and remain dependent on their mother for a long period. Differences in the maternal behaviour of injured and non-injured mothers affected their older dependants. Juveniles with injured mothers were more often found at distances further from their mother than juveniles with non-injured mothers. Dependants of injured mothers were less likely to be carried when compared to those of non-injured mothers, but very young infants had the same level of maternal care, whether or not they had injured mothers. Any lack of maternal care for very young chimpanzees would be serious; it could even influence the survival of the offspring.

## **Chapter 6 - Grooming behaviour**

Grooming has an important role in chimpanzee society for both hygienic and social purposes. Injured mothers both groomed, and were groomed by, their dependants to the same extent as non-injured mothers. Injured females received as much grooming as non-injured females did from community members other than their dependants, but they groomed others less frequently than non-injured females. Injured females had fewer adult male grooming partners.

## **Chapter 7 - Locomotion**

The ability to travel distances on the ground and to move freely in the trees is crucial to the survival of chimpanzees. Injured female chimpanzees travelled both on the ground and in the trees, and utilised all parts of arboreal space. Despite this, they were more cumbersome in their locomotion, and used modified forms of the locomotion seen for able-bodied chimpanzees. The most severely injured chimpanzees spent less time moving when compared to all other chimpanzees, and all injured chimpanzees moved less on the ground than non-injured chimpanzees. Injured chimpanzees also spent more overall time in the trees suggesting a preference for arboreal space.



## 8.2 Discussion of Results

The discussion of results, for each chapter, has revealed the same overall conclusion: it is the physical difficulties associated with an injury that are responsible for the differing behaviours seen, rather than any apparent discrimination against injured individuals by able-bodied chimpanzees.

The main physical difficulty for injured chimpanzees is that their locomotion is more cumbersome. Even though injured chimpanzees were able to move both on the ground and in the trees, locomotion was more difficult for injured chimpanzees. Injured individuals used modified versions of locomotor types seen for able-bodied chimpanzees. They would sometimes lose their balance, and would move more awkwardly, than non-injured chimpanzees. The most severely injured females spent less time moving than other chimpanzees, and all injured females spent less time moving on the ground than non-injured chimpanzees. Injured females carried their older dependants less than a non-injured mother; they were evidently less able to carry the dependant as it became heavier. Injured females spent more time in small and family groups; the physical difficulties associated with long distance travel mean that injured females may be less able to keep up.

Reducing feeding competition is another major reason why injured females behaved different from non-injured females. Injured females did not spend more time feeding than non-injured females, suggesting they had a similar ability to process foods, but perhaps they had physical difficulty in gaining access to the best foods when in the presence of a large group. Some foods, such as *Ficus sur*, a common fig species used by the chimpanzees at Sonso, were difficult for injured females to feed on since the figs are suspended from a branch in large clumps. Able-bodied chimpanzees commonly hang from the large clump by one hand, and one or two feet, while using the other hand to process the figs. An injured female may require a seated position to access these figs, and may be more confident doing this when other chimpanzees are not attempting to feed off the same clump. For other food types, it may be that injured females have one or two fewer limbs to help with balance in arboreal space, and so it is easier to access food when in

the presence of fewer competitors. So a reduction in feeding competition is a result of the physical difficulties associated with a limb injury; in this case, a lack of balance. I frequently observed that injured females fed alone or in small groups, after the majority of the group had moved off to another site. Injured females spent more time in small and family groups, and more time arboreal; this supports a hypothesis that they were remaining in a feed tree long after other group members had travelled off in order to reduce feeding competition. Female chimpanzees have been shown elsewhere to spend time alone, or in small groups, in order to reduce feeding competition (White & Wrangham 1988; Wrangham & Smuts 1980). Perhaps injured females behave in this way even more than non-injured females in order to further reduce their competition for food.

A third reason why injured females behaved differently to non-injured females may have been fear of ground travel. Injured females may feel more vulnerable to predators on the ground, because of their difficulties in locomotion. A memory of being snared on the ground may also add to an injured female's fear of ground travel. Injured females did spend less time travelling on the ground, and more time 'left behind' in smaller groups.

There seems to be no lack of tolerance by other community members toward injured females. The possibility that able-bodied individuals may discriminate against those that are injured was considered as an explanation for why injured females may behave differently from non-injured females. This hypothesis is not supported in this thesis.

Injured females did not show any differences in patterns of female-female association. Also, other community members groomed injured chimpanzees as often as they did non-injured chimpanzees, and injured chimpanzees travelled and spent time with all age/sex classes, for at least some of the time they were observed. The only possible suggestion of intolerance was that adult males infrequently had injured females as grooming partners. This may be more to do with their lower association with injured females, than with any lack of tolerance. Once again, this relates to physical difficulties. The reason why injured females had a lower association with adult males is because they spent more time in small

groups, or alone with their dependants, and so had fewer opportunities to associate with males. The reasons why injured females spent time in small groups are all related to their physical disabilities (see above). There is no reason to believe that injured females spent time in smaller groups because other community members did not tolerate them in their own groups. General anecdotal observations of the chimpanzees of the Sonso community also support the idea that injured chimpanzees were well tolerated.

All the above examples suggest that throughout this thesis the behavioural differences seen are related to the physical difficulties associated with an injury, rather than any lack of tolerance shown by other community members.

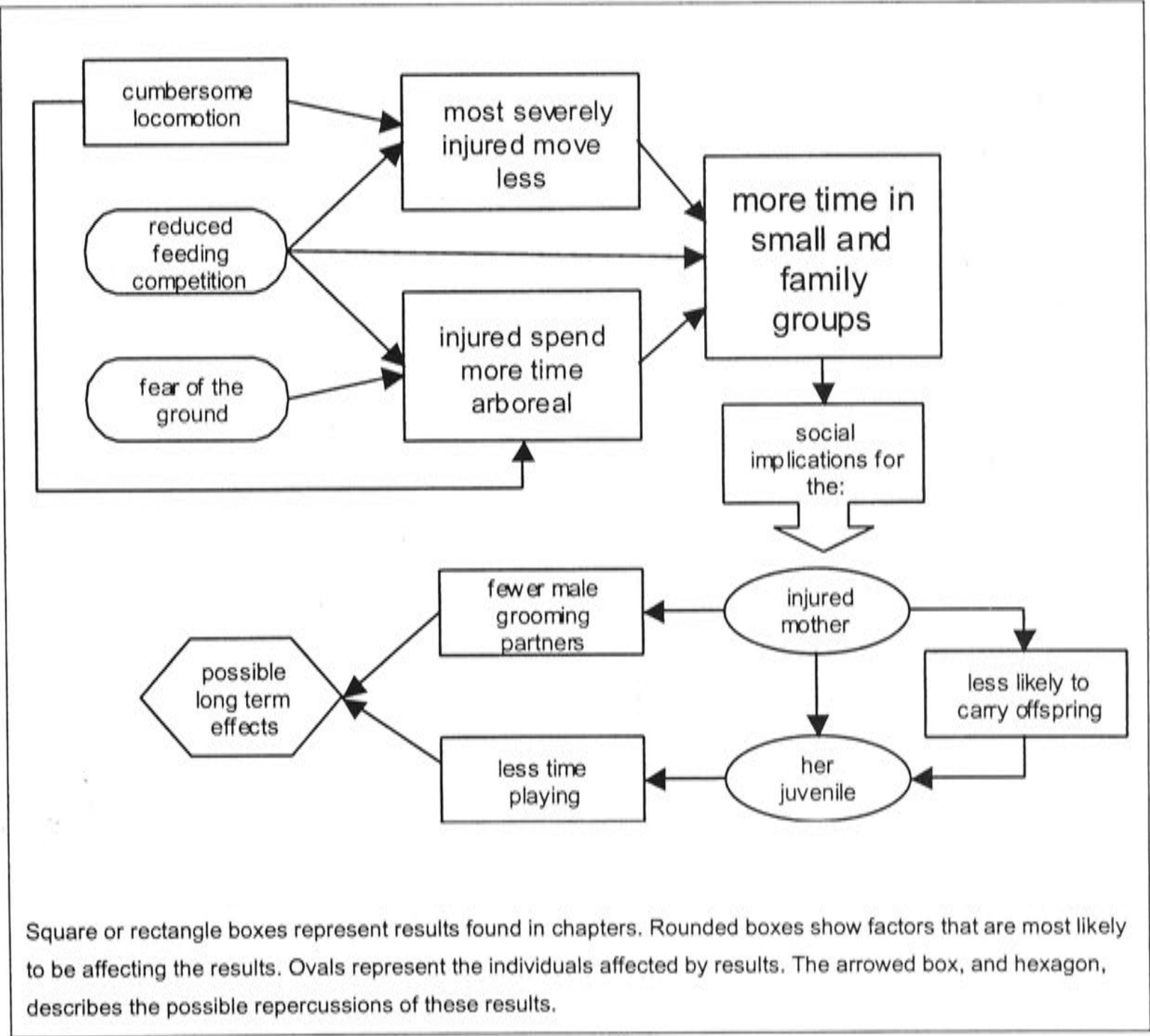
Although it is the physical difficulties associated with an injury that cause differences in behaviour, these differences have the potential of impacting on the social opportunities for an individual. Many of the behaviours discussed above result in injured females spending more time in small and family groups (see Figure 8.1). That injured females are more commonly alone, and less commonly in large mixed-sex groups, has the potential of impacting on the social opportunities of both the injured females and their offspring. This is probably why injured females had fewer adult male grooming partners. The offspring of injured females may also be socially affected; juvenile offspring of injured mothers spent much less time playing with others than did those of non-injured mothers. This may be affected by the injury of the mother in two ways: because of the more solitary nature of injured mothers, and because of the additional demands placed on offspring of injured mothers. Juvenile 1 offspring are at an age where they are more independent of their mothers, being able to feed and travel by themselves, yet remaining in the same group as their mother. In this study, these offspring were given less support by the mother if she was injured. This may result in less time for activities such as play. Either way it is the injury of the mother, directly or indirectly, that may cause their juveniles to play less than juveniles with non-injured mothers. Furthermore, the offspring may suffer longer-term social repercussions.



As well as negative social implications, there are also other factors that may impact on the overall well-being and survival of injured chimpanzees. Individuals who spent more time in small groups, or alone with dependants, are at an increased risk of predation or infanticide. This has an impact on the survival of individual chimpanzees, and so the overall population growth may also be affected.

The results from all chapters in this thesis are inter-related. The discussion above reveals that the same causal factors are responsible for many of the results found. Figure 8.1 summarises how the results are inter-related, and how the physical

**Figure 8.1** Flow chart summarising how results are inter-related for injured female chimpanzees with dependants of the Sonso community



difficulties associated with an injury can lead to social implications, and possible long-term affects.

Possible long-term effects may include: an increased risk of predation and infanticide for injured females and their offspring as they spend more time alone; a reduced reproductive rate for injured females if they are spending less time with adult males; and offspring may have a lower dominance rank as they get older since they spent less time socialising when young. These effects, coupled with the fact that some chimpanzees die from snare wounds, may result in a lower population growth. This impacts on the overall long-term survival of an endangered species.

### **8.3 Implications for palaeoanthropology**

From this study, it is evident that injured chimpanzees were shown a degree of tolerance by other community members. Tolerance, or respect, has been described elsewhere as the “free flow of information concerning local resources” and an “undifferentiated response across categorical divisions”, and not an issue of “physical care or special kinds of social support” (Quiatt et al. 1994, p.8). There were no signs of other community members actively helping, or supporting, injured individuals in any way at the Sonso community. That chimpanzees survive in communities with only a level of tolerance shown by others, rather than any active support, may have implications for palaeoanthropology.

Earlier in this thesis the discovery of hominid fossils with disabilities was discussed (section 2.3). Some writers argued that these discoveries showed evidence of compassion and moral decency in these prehistoric communities (Dettwyler 1991). De Waal (1996) argued that the case of Mozu, the Japanese macaque, did not prove there was any evidence of moral decency amongst the macaques; only a degree of tolerance was shown. Likewise, the survival of disabled fossils in a community can confirm only tolerance between individuals (de Waal 1996). The injured chimpanzees in this study received no special care from others in their community and managed to survive, even with, in some cases, extreme deformities. This supports de Waal’s (1996) comments and results

previously discussed by Quiatt et al (1994). Tolerance, shown by other community members, assists the survival of injured chimpanzees in the Sonso community, but this does not necessarily reflect moral decency or compassion.

Although there were no observed signs of active support in the Sonso community, such behaviours have been described for other chimpanzee and gorilla communities. Individuals have been observed to remove a newly embedded snare from a victim at Parc National des Volcano, Rwanda and at Taï National Park, Côte d'Ivoire (sections 2.2.3 and 2.2.5.1). Other examples of active support include physical assistance during feeding or locomotion. This was not observed for the Sonso community, but anecdotal evidence suggests that chimpanzees in the nearby Kasokwa Forest Reserve assisted a male chimpanzee caught in a steel jaw trap by shaking mangoes from a tree (Munn & Kalema 1999-2000). Perhaps these examples do suggest evidence of compassion.

#### **8.4 Snare injuries vs. congenital deformity**

Of the five injured chimpanzees in this study, four have injuries from snares and one, Banura, has a congenital deformity. Banura was included as an "injured" mother, despite the fact that her deformity was not the result of being injured. This was because her handicap showed signs of affecting her behaviour, similar to the snare-injured mothers. Physically her disability was equivalent to snare-injured chimpanzees; she had no use of the digits of her foot, or the actual foot itself. This affected her movement and her balance, and made her locomotion more cumbersome, as was the case for the other handicapped chimpanzees. Socially her disability may have been different. Since she was born with her injury, other community members may have accepted her to a greater or lesser degree, than mothers who received their injuries later in life. This was not the case. All handicapped chimpanzees, Banura included, were well accepted into the broader community. Lack of tolerance was not the causal factor of the differences seen between injured and non-injured chimpanzees' behaviour.

Results from the analyses showed that on a couple of occasions Banura was less affected by her deformity than the other injured females. For example, Figure 4.1



shows the number of scans spent in either small or large groups, as a percentage of total number of scans. In this figure Banura is the injured mother most like the non-injured set, spending more time in larger groups than the other four injured mothers. Figure 4.11 shows the number of scans spent within 1m and within 5m of at least one other individual. Banura spent more time within 5m of at least one other individual than other injured mothers. Once again, this result was similar to the non-injured data set. These results suggest that, if anything, Banura's inclusion in the "injured" set reduced the level of affect shown by injured chimpanzees. Although these examples show that Banura was like the non-injured set, on some occasions there were analyses where other injured females (e.g. Keway and Kalema) showed behaviour most like the non-injured set. Overall, it appears that Banura was well placed in the injured set.

Banura, with her life-long disability, was similarly affected by her handicap when compared with other chimpanzees that were injured by snare wounds later in life. This is further support for the conclusion that it is the physical difficulties associated with being handicapped that ultimately affects behaviour patterns, rather than a lack of tolerance shown by other group members.

Because 90% of the disabilities seen in the Sonso community are directly attributable to snares, this thesis also discusses the conservation implications of snaring, and how a reduction in snare injuries could be achieved. Congenital deformities will always be a part of chimpanzee society, and individuals with such disabilities will continue to show signs of behavioural impairment whether or not snaring is reduced in African forests.

## **8.5 Number and extent of injury**

Three of the Sonso chimpanzees have snare injuries to more than one limb. Zana and Tinka have injuries to both hands, and Shida has both an injured hand and foot (see section 2.2.5.2). Zana was the only study female with more than one injury. Injury appeared to have more severe effects on the general locomotion, feeding and grooming behaviour of these three individuals, when compared to other injured or able-bodied chimpanzees. In particular, Shida had obvious

difficulty moving both on the ground and in the trees. Having one foot and one hand severely injured seemed to be even more disabling than having two hands injured. Shida would find life even more difficult were her two injuries on the same side of her body, and it is likely that life would become impossible if she gained a third injury.

The severity of an injury also affected the level of behavioural impairment seen among injured chimpanzees. Zana and Kigere had the most severe injuries out of the five injured study females; Zana had two severely injured hands, and Kigere was missing her whole foot. Both had obvious difficulties with movement, and both would sometimes lose their balance when in the trees. This is potentially life threatening for a chimpanzee. Zana and Kigere spent less time moving, and less time moving on the ground, than all other females. They also spent the most time in arboreal space. As would be expected, the more severe the injury the greater the physical effects seen. These two females spent more time in small groups, or alone with dependants (as did all injured females). This has social repercussions such as that Zana and Kigere had fewer grooming partners than other injured females, and Zana spent the lowest amount of time within 5m of at least one other community member.

Snare injuries are still occurring in the Budongo Forest. One chimpanzee was injured during the study period – a sub-adult male, Gershom, was first seen with a wire snare around two fingers of his right hand on 2<sup>nd</sup> March 2000 (personal observation). Two chimpanzees have received snare injuries since the end of the study period – an adult male, Zefa, was first seen with a snare on 19<sup>th</sup> September 2000 (see Figure 1.1), and a juvenile female, Betty, was first seen with a snare on 18<sup>th</sup> April 2002 (F. Babweteera, personal communication). While snaring continues in Ugandan forests, so too does the problem of chimpanzees becoming trapped in snares, and the resulting injury or death. Chimpanzees with one snare injury are at a risk of receiving a second injury; further increasing the impact that injury has on their behaviour. Chimpanzees with two injuries may receive a third, placing enormous pressure on their ability to survive. Although there is the recorded case of Mozu, the Japanese macaque, surviving with four injured limbs

(see section 2.2.1), it seems doubtful that a chimpanzee, receiving no artificial provisions, could survive in the wild with injuries to more than two limbs.

The greater the number and extent of the injuries, the greater impact these injuries have on the behaviour, and survival, of injured chimpanzees.

## **8.6 Implications for conservation of an endangered species**

Ninety percent of physical deformities in the Sonso community are a result of individuals being caught in hunters' snares. As described above, so long as snaring continues, the risk of injury or death from snare wounds also continues. Further, those individuals that have already received an injury are at risk of gaining a second or third injury.

As described in Chapter One, there are many threats to the survival of chimpanzees in Africa. Some, such as the bush meat trade in west and central Africa, result in the death of countless chimpanzees. In contrast, snaring has resulted in only a few known deaths (Boesch & Boesch-Achermann 2000; Munn & Kalema 1999-2000; Wrangham & Mugume 2000), and despite the many injuries that are occurring, most injured chimpanzees are surviving and reproducing. This study has shown that injured females from the Sonso community do behave differently from non-injured females, and it is possible that their more solitary existence may lead to long-term social repercussions. These could include a lower reproductive rate, since injured females spent less time in large mixed groups and have fewer male grooming partners (although all injured females in this study have at least one dependant offspring). Long-term effects may also include an increased risk of infanticide or predation since injured females spend more time alone. Two cases of infanticide have previously been described for the study community (Newton-Fisher 1999), and in the present study two cases of adult males carrying infants possibly snatched from a neighbouring community were recorded (Notman & Munn 2003). These factors, together with deaths from snare wounds, all lead to a reduction in the potential size of a community. A population modelling simulation of chimpanzees in Uganda determined that in a population of 100 individuals the annual removal, by human-



caused mortality, of one single female and her dependant offspring could have “ a real detrimental effect on the growth potential of chimpanzee populations” (Edroma et al. 1997, p.71). Although it is unknown if snaring is causing this level of mortality, this suggests that deaths known to occur from snaring *are* having an impact on the growth potential of a population.

The low incidence of deaths from snaring is probably because snaring of chimpanzees in Uganda has mostly been accidental. All hunting of vertebrate species living within Uganda’s forest reserves is against the law (Howard 1991), and it is considered culturally unacceptable to eat primate meat for almost all Ugandans (Johnson 1996). This excludes the Batwa, Baamba, Bakonjo and Bagisu ethnic groups who hunt primates when in their traditional areas, including Semliki, Rwenzori and Mt. Elgon (Howard 1991).

Snaring may, unfortunately, be on the increase in Ugandan forests. Firstly, this is because of the expanding human population. Uganda has an annual rate of population growth (without regard for migration) of 3% (Population Reference Bureau – World Population Data Sheet, 2002). The population in Uganda in mid-2002 was 24.7 million. This is expected to almost double to 48.0 million by 2025, and then by 2050 an expected 84.1 million people will be living in Uganda (Population Reference Bureau – World Population Data Sheet, 2002). Population pressure creates an increasing demand for all forest resources including bush meat, and the accidental snaring of chimpanzees is likely to increase as a result. Secondly, there has been an influx of ethnic groups into Uganda. The instability in the Democratic Republic of Congo (DRC) has led to hundreds of refugees crossing the Ugandan border in hope of finding security. Nearly one-third of immigrants from the DRC living in a village near the Budongo Forest are known to eat primates (Johnson 1996), although it is unclear if this included chimpanzees. Until recently, no known deliberate hunting of chimpanzees for trade or meat in Uganda had been recorded. A recent unpublished report tells the tale of two bush meat traders who were arrested carrying chimpanzee carcasses in western Uganda (Moeller 2000). It is possible that the bush meat traders were Congolese, and so hunting for themselves. Alternatively, they could have been

hunting to supply a new market that may be opening in Uganda that reflects the traditions and habits of refugees, the eating of primate meat being one of them.

Deaths and injuries to chimpanzees will certainly increase as the human population increases, and as more immigrants, with no cultural taboo on eating primates, arrive in Uganda. As injuries affect the survival, behaviour, and welfare of chimpanzees, efforts must be made in order to reduce, or eliminate, the occurrence of snaring in Ugandan forests.

## **8.7 Ways of reducing snaring in Ugandan forests**

In order to decrease, or eliminate, snare injuries to chimpanzees, programs need to be established to reduce the level of snaring in Ugandan forests. There are already some successful programs in different parts of Uganda.

### **8.7.1 Existing programs**

#### **Kibale**

A snare removal program was established in Kibale National Park, in the Kanyawara region, in September 1997 (Wrangham & Mugume 2000). Initially, a snare patrol team covered only the home range of the Kanyawara chimpanzees, although now around 50% of the park has been searched (Wrangham & Mugume 2000). Since the program began, up until June 2000, a total of 2290 snares were removed. This is around 67 snares per month (Wrangham & Mugume 2000). There has been a two-year period with no snare injuries at Kanyawara, and there is some indication that the rate of snare finding is decreasing (Wrangham & Mugume 2000). These results suggest that the snare removal program is contributing to the welfare of chimpanzees. Despite these intensive efforts, chimpanzees in the Kanyawara community are still at risk from snares as a fresh snare wound occurred in April 2000, breaking the two-year period of no injuries from snares (Wrangham & Mugume 2000).

## **Budongo**

A snare removal program was initiated in the Budongo Forest in the home range of the Sonso community of chimpanzees in January 2000. Two local ex-hunters were trained and outfitted with equipment for effective snare removal. In the first three months of the program the pair removed 514 snares from the forest (see end of section 2.2.5.2). There was a negative response from local hunters; some research items in the forest were stolen or destroyed in response to the snare removal program. For this reason the program was temporarily halted. An education program was then set up to inform hunters and local people about the importance of the snare removal program. Later, in 2000 the snare removal program was re-started while the education program continued. Since that time, two workers go into the forest on a regular basis and remove several snares each day. Man-traps (large steel-jaw traps) have also been found and removed from the forest. Each time a snare is found its location is recorded using a GPS (V. Reynolds, personal communication).

### **8.7.2 Future ideas**

Snare removal programs such as the two described above are a crucial component of reducing snare-related injuries. Alongside these programs several other programs need to be created. Education programs are vital in allowing local people to understand the need for snare removal programs, and the long-term importance of forests. General public awareness regarding chimpanzees and the protection of endangered species is also necessary. Information leaflets should be provided in local languages, and follow up talks and question times should be part of any program. It is also important for people living near forest areas to feel as if there is some kind of benefit to them personally from any type of forest conservation. Employment is one such way this can be achieved. Hunters can be trained as snare removal rangers, as has been the case at Budongo, or trained to become rangers in National Parks or Forest Reserves. It is possible that hunters could use their positions to continue to set snares in the forest, although this did not seem to be the case for the two ex-hunters employed at Budongo. Small farms breeding species such as rabbits or cane rats could be created which would



provide both employment and additional protein sources to replace bush meat. Alternatively, hunters could be employed to make traditional arts and crafts to sell to tourists in the area. Tourism plays an important part in getting direct benefits from forest wildlife. An increase of tourists increases money coming to an area, and employment for local people. Tourism can also bring problems of a potential disease threat from humans to apes (Wallis & Lee 1999), and so must be managed carefully.

A population and habitat viability assessment (PHVA) for chimpanzees in Uganda was conducted in 1997. This describes snaring and other forms of poaching as major threats to the survival of chimpanzees in the country (Edroma et al. 1997). Solutions to this threat included those already mentioned, as well as negative publicity about eating chimpanzees (linking primate consumption and the Ebola virus), studies into the effectiveness and feasibility of different approaches of eliminating snares, and designing chimpanzee-friendly snares which minimise injuries (Edroma et al. 1997).

These programs and solutions are essential in order to reduce the threat placed on chimpanzees in Ugandan forests. It is important to remember that when any of these programs are being designed or undertaken, the needs of local communities must be taken into account. Local people use the forests for many resources including bush meat, firewood, building materials, food and medicines. Their cooperation is essential for a successful program of any type.

There are also broader solutions including habitat protection, and reducing human population growth in order to reduce the pressure placed on limited resources. In a study which looked at the micro-demography of villages adjacent to the Budongo Forest Reserve, it was found that only 1 in 3 women had heard of family planning, and that only one woman of the 99 interviewed had ever used this knowledge (Marriott 1996). The issue of contraception is a sensitive one. While traditional views on fertility prevail, some women interviewed did express an interest in family planning. Reasons given were the number of pregnancies they had experienced, the difficulties in delivering, and maternal illness (Marriott 1996).

Many of these programs will take considerable financial and logistical commitments. In terms of the survival of chimpanzees, and also the reduction of snare related injuries and deaths, it is essential that programs such as those outlined above be given serious attention.

## **8.8 Hope for Uganda**

Although chimpanzees are threatened with extinction in Uganda and other countries, there are factors that give Uganda hope for the long-term survival of its chimpanzees, and the possible success of conservation and education programs.

Firstly, Uganda has a population of around 4,500 chimpanzees (Plumptre et al. 2003) spread across 12 forest blocks (Edroma et al. 1997). In comparison, neighbouring countries have fewer chimpanzees, or less well-protected chimpanzees. For example, Tanzania's chimpanzees are protected in only two parks, Gombe National Park and Mahale Mountains National Park. Burundi and Rwanda both have low numbers of wild chimpanzees and extermination of these populations is expected soon (Teleki 1989). In the Democratic Republic of Congo (DRC) political instability has wiped out most protection of wildlife and the forests.

Secondly, many African countries have the problem of limited investment into National Parks. In many countries, parks are being heavily degraded (e.g. Tai National Park, Ivory Coast) or reduced in size (e.g. Bia National Park, Ghana: 306km<sup>2</sup> in 1974, and then 77.7km<sup>2</sup> by 1980) (Chapman et al. 1999). Uganda is in a fortunate position. The amount of protected land has increased from 7698 km<sup>2</sup> in the 1980s to 11145km<sup>2</sup> as of 1995 (Chapman et al. 1999); although, as in many regions of Africa, the lack of funding for protected areas leads to little enforcement and education of existing wildlife laws, so hunting and encroachment still occur in protected areas.

Uganda has great potential for wildlife and forest conservation. Uganda's President, Yoweri Museveni, supports forest conservation, and the press promote care and conservation of chimpanzees (Wrangham 2001). A number of



governmental and non-governmental organisations have greatly reduced the international pet trade in chimpanzees, as well as developing sanctuaries for orphan chimpanzees (Wrangham 2001). Tourism supports placing conservation as a high priority, with money coming directly from wildlife visitation (as in the case of mountain gorillas and chimpanzees), as well as money being injected into local communities through employment and from sales of arts and crafts, and also local produce, to tourists. During the years between 1990 and 1997, the tourism sector in Uganda registered an annual growth rate of over 10% (NEMA 1999), although a drop in tourist numbers occurred in 1999 after the tourist kidnapping at Bwindi National Park (Archabald & Naughton-Treves 2001).

It is hoped that the above factors – namely the numbers of chimpanzees in Uganda, the areas of forest set aside for protection, and the government support for conservation – will help in future efforts to protect forest areas and promote chimpanzee conservation.

## **8.9 Directions for future research**

Results in this study apply to the injured adult female chimpanzees of the Sonso community. They do not necessarily relate to chimpanzees living in other locations, or chimpanzees of any other age/sex classes. Results in this thesis suggest that all injured chimpanzees may show some form of behavioural impairment because of injury. A comparative study of adult females from other communities in Uganda would strengthen results found in this thesis. Also, studies across different sites, focusing on the effects of injuries on adult male chimpanzees, or other age/sex classes, would give a broader understanding of the effects of injuries on chimpanzees. For example, data collected on adult males, relating to grouping patterns and association, would provide results different from data collected in this study. Association and grouping are known to differ between sexes (see section 4.2.1 and 4.2.2).

Long-term data are essential in understanding the implications of the behavioural changes seen among the adult female chimpanzees of the Sonso community. Data on inter-birth intervals, infant survival, female ranging and dominance behaviour,



are vital in order to determine whether injured chimpanzees have a lower reproductive success, which may affect overall population growth. Data on when injured females are in oestrus is also important to determine whether, at these times, they do spend more time in larger groups, and so more time with adult males.

Long-term data are important for studying the effects of injuries on younger chimpanzees. For example, the juvenile female Shida, who has two severe injuries, may develop differently from a non-injured juvenile. In particular, she may have difficulties if transferring to a neighbouring community. I predict that she is likely to remain with her mother, regardless of if she would have otherwise immigrated.

Research is also necessary to determine the effectiveness of snare removal, education and other programs set up to eliminate snaring in Ugandan forests. Such research was recommended in the Population and Habitat Viability Analysis (PHVA) carried out for chimpanzees in Uganda in 1997 (Edroma et al. 1997).

## **8.10 Final Conclusions**

In conclusion, adult female chimpanzees of the Sonso community are affected by their injuries. Their ability to travel, including both the time spent moving and types of locomotion used, is altered when compared with that of able-bodied chimpanzees. Grouping patterns are different; injured females show a preference for small groups and family units. The relationship with their offspring is affected since injured mothers have difficulty carrying older dependants, and juveniles of injured mothers spent less time in close proximity to them. Finally, changes in grooming behaviour are evident since injured females groomed other community members less, and had fewer adult male grooming partners. Other community members did not show any lack of tolerance toward injured females. Rather, the physical difficulties associated with having an injury explain the differences in behaviour seen.

The results in this thesis may have long-term consequences for injured females, such as a lower reproductive rate, or an increased risk of predation or infanticide.

Either way, overall population growth may be affected. This has implications for the conservation of an endangered species. For this reason, as well as for the general welfare of injured chimpanzees, snaring needs to be reduced in Ugandan forests. Without programs set in place for the reduction of snaring, levels will increase. The time to act is now, while there is still hope for the survival of chimpanzees in Uganda.

## Appendix 1

### Female-female association – difference between studies

Results from female-female association data in the present study revealed much higher Dyadic Association Indices (DAI) than found elsewhere. For example an average DAI of 0.11 was recorded at Tai, 0.05 at Gombe, 0.08 at Kibale (Boesch & Boesch-Achermann 2000) and 0.17 at Kibale, during a two-month period when party size was greater (Wrangham et al. 1992). These compare to an average DAI of 0.23 in the present study. There are two main factors which together account for the difference:

1. the present data were collected only on females, and so a female bias is apparent.
2. the present study revealed a higher percentage of nursery groups than other studies.

### Female bias

The present study collected data in a female-biased way. The 12 study females (all adult females with dependants, most non-cycling – see section 6.7.3) were actively sought out, and data were not collected until a study female was located. If we first encountered a group without study females, we would move on to search for others, without collecting any data on the first group. On some occasions, if searches for a study female were not successful, we would return to the main group and hope that a study female would join.

In contrast, females are undersampled in all previous field research on chimpanzees (Pepper et al. 1999). Most chimpanzee studies are biased towards large mixed groups: either because male behaviour is being studied, because it is easier to follow a large group, or because more data can be collected on a greater number of individuals if the main group is being followed. Males, oestrus females and cycling females tend to group in large mixed and sexual groups more often



than non-cycling females with young (Matsumoto-Oda 1999). It is the tendency for non-cycling females to spend time alone with their young or in nursery groups (Goodall 1986).

If an observer is focusing on the main group of chimpanzees it is likely that they are creating a bias towards observing males and cycling females. In fact Boesch and Boesch-Achermann (2000) stated that, as they were mainly interested in the main group of parties, they often left small groups of females alone, and thus the DAI's of the females that they recorded would underestimate the time particular females spent together (Boesch & Boesch-Achermann 2000).

A further study at Tai Forest confirmed that the primary research focus did play a large part in the results obtained. While Boesch followed main groups for the purpose of observing hunting and nut cracking behaviours, Doran (1997) had an even focus on males and females, rotating between the sexes in order to document positional behaviour, and her study uncovered very different patterns of grouping. Doran suggested that differences in choice of the target accounted for at least some of the difference in the results seen (Doran 1997).

The present study has a female bias; only females were followed, in order to gain specific information about that sub group, so there is also a bias towards the groups that females most commonly form (see below).

#### Nursery groups

Pepper et al. (1999) discuss the fact that although many studies note the regular occurrence of nursery groups, little attention has been directed towards these groups in comparison to data available on all male groups. The authors suggest that nursery groups are not "passive aggregations" (p.624), as has been previously noted; rather the females in these groups show strong female-female bonding (Pepper et al. 1999).

Table A1.1 shows that in the current study, a higher number of nursery groups were recorded when compared to two other studies from Budongo, where data

were collected on both males and females (Fawcett 2000; Reynolds & Reynolds 1965). The percentage of nursery groups was similarly low for two studies from other field sites where both male and female data were collected (Boesch & Boesch-Achermann 2000; Matsumoto-Oda et al. 1998). On the other hand, studies with a female focus (or where female data was analysed separately to male data) show a higher proportion of nursery groups (Doran 1997; Halperin 1979). This is consistent with the higher number of nursery groups observed in the present study, when females were the focus.

The female bias in this study means that a greater proportion of nursery groups were observed. In the past, the finding of low rates of female-female association has led to the suggestion that nursery groups are uncommon (Wrangham et al. 1992). The reverse, that high association between females must correspond to a higher proportion of nursery groups, should also be true. So it is possible that the higher DAI's recorded in this study are a factor of the high number of nursery groups observed.

Table A1.1 also shows that the number of lone-female groups in the present study is less than in two other female focused studies. This is likely to be because of differences in habituation levels, with females at Budongo being less habituated, so more difficult to observe when alone. The lower levels of lone females in the present study would increase the association level seen between females, as females were more often observed with other females and so in association, rather than in the Taï and Gombe study, where they were more often seen alone. The low numbers of solitary females observed in this study would further increase the DAI recorded.

Caution must be taken in comparing the data in Table A1.1 as different methods are used in studies, and other factors such as length of study, and time of year of study (i.e. different resources available) are known to impact on grouping. Also exact definitions of terms may differ between studies.



**Table A1.1** Percentages of different social group compositions

	<i>Budongo (current)</i>	<i>Gombe</i>	<i>Tai (1)</i>	<i>Budongo (1)</i>	<i>Budongo (2)</i>	<i>Mahale</i>	<i>Tai (2)</i>	<i>Gombe</i>	<i>Tai (1)</i>
Focus of study (Male/Female)	F	F	F	M/F	M/F	M/F	M/F	M	M
<i>Group type</i>									
Mixed/Sexual	54.5	9.6	18	67.4	67.6	63	51.2	47.1	56
Female/Nursery	34.4	25.4	37	16.7	16.8	17	17.7	-	-
All Male	-	-	-	15.8	11.3	9	20.0	23.2	18
Lone females	11.1	65	45	-	-	2	4.3	-	-
Lone males	-	-	-	-	-	9	6.5	29.6	26

Budongo (current): present study

Budongo (1): Reynolds and Reynolds (1965), percentages calculated from data given in table.

Budongo (2): Fawcett (2000)

Gombe: Halperin (1979), percentages calculated from data given in tables

Mahale: Matsumoto-Oda et al (1998), percentages calculated from data given in table and text.

Tai (1): Doran (1997), mixed sex and lone percentages given in table, others estimated from figure.

Tai (2): Boesch and Boesch Achermann (2000)

N.B. some figures in this table were derived by adding together different categories, such as adult groups with mixed sex and sexual groups to come to the total for mixed/sexual given above.

Other contributing factors

The standard association measure – the Dyadic association index – that is used in almost all studies of association relies on determining the number of occasions that two individuals are seen together as a proportion of the total number of occasions that either of the individuals is seen. In any group each individual gets one count of association with each other individual in the group. So in large groups each individual will gain more counts of association per group than in small groups. Therefore if a particular age/sex class prefers either large or small groups, and we are trying to determine the association of a particular age/sex, then



the results will be greatly affected by the preference. Individuals that prefer small groups will gain fewer overall points of association than individuals that prefer large groups, and may thus appear to have lower association indices. This does not mean that they do not prefer particular other individuals.

Pepper et al (1999) discuss these issues in more detail arguing that previous studies of chimpanzee grouping patterns have overlooked two major problems in their methodology. Firstly association levels have been used to directly infer social preferences, and secondly social preferences have not been measured independently of general gregariousness (Pepper et al. 1999). A low frequency of all-female groups observed could suggest weak female bonds when using a DAI, but may simply be a factor of all-female groups being in small groups. Further if males are more commonly found in large groups than females, this will result in more frequent male- male associations than female-female association, regardless of whether males have an association preference for other males (Pepper et al. 1999). Several statistical tests and indices are provided to control for these problems (Pepper et al. 1999). Using these tests Pepper et al. (1999) found that, when the differences in gregariousness between different age/sex classes were controlled for, anoestrous females had strong affinities for each other, and association between adult males was due more to their greater gregariousness, rather than to a "specific pairwise affinity" (p.624).

In the present study there was a high frequency of all females groups, and so higher DAI were seen. The present study did not include focal data on males and so the indices used in Pepper et al (1999) could not be used with the present data.

A further issue that may affect the DAI's recorded in this study is its short-term nature. The study period was eight months (see Chapter 3). It is possible that the association patterns of the females was a reflection of food availability, or some other external factor that was operating during that time.

It appears that all, or some, of the above factors have contributed to the high female-female association levels seen in the present study. The fact that only

females were observed as focals in this study led to a larger proportion of nursery groups observed, which in turn resulted in greater association indices between females. Lone females with dependants were less frequent in this study than at other sites (where data were analysed separately for males and females), which results in an increase in the DAI. The bias inherent in using DAI (Pepper et al. 1999) means that previous studies have perhaps underestimated the association levels for females, and although this study shows its own strong bias, it does suggest that female-female association is in fact higher than previously recorded. This would only be seen when taking into account the differences in gregariousness between different age, sex and reproductive classes (Pepper et al. 1999), or when the study has a complete bias towards female subjects.

## Appendix 2

### **Dominance hierarchy between adult females of the Sonso community**

Although it is clear that some females dominate others, social ranking and dominance is difficult to determine for female chimpanzees (Nishida 1990; Pusey et al. 1997). This is because some females rarely meet (Nishida 1990), dominance behaviour is uncommon such as aggressive behaviour (Pusey et al. 1997), and pant grunting (a well recognised behaviour for determining dominance hierarchy) is rare among females (Nishida 1989).

In the present study very few dominance interactions between adult females were observed. Dominance interactions were recorded as part of event data and both threatening and attacking behaviours were observed. The definitions of these behaviours is as follows:

Threaten: by gestures, postures or calls with no physical contact. Includes hair bristling, vocalisations, branch swaying, bi-pedal swagger, stamping, slapping ground, and charging.

Attack #1: attack on another individual in passing, actual physical contact, short lived, ie. run and hit in passing

Attack #2: attack lasts less than 30 secs, a brief pounding, hitting or rolling

Attack #3: attack lasts longer than 30 secs, more severe

Pant-grunting was recorded in a larger category of vocalisations, so is unable to be determined from the present data.

Very few records of agonistic interactions were observed during observation periods, so it is not possible to determine dominance from these events alone. A previous study from Budongo Forest did record both agonistic interactions and



pant grunts between females (Fawcett 2000). One hundred and two dominance interactions were recorded between female chimpanzees, although this also included sub-adult females. There were substantially more dominance interactions between sub-adult females and other females, than there were between adult females (Fawcett 2000).

Combining adult female data from Fawcett (2000) and the present study it is still difficult to establish any clear hierarchy (see Table A2.1). Difficulties arise because there are many individuals that were not observed in any agonistic interactions, and there are many dyads that were not recorded having any aggressive interactions. Also data from each study were recorded at different times and dominance changes with age and time. For instance Janie was a sub-adult in Fawcett's (2000) study, and was an adult in the present study. Her ranking seems to have risen greatly during the time between studies. Keway, on the other hand, has also become an adult since Fawcett's study, although there is not a similar rise in rank recorded for her. The rankings given in Table A2.1 are therefore ambiguous and much more data is required on interactions between adult females to determine a true hierarchy.

It was strongly established that Nambi (NB) was the most likely alpha female having dominated more individuals and was dominant in more interactions than any other female (Fawcett, 2000). This was also the case in the present study, as well as from general field observations.

As the dominance hierarchy is as best suggestive it is not possible to determine if grooming, or other behaviours are affected by the rank of the individual.

Both injured and non-injured females are both high and low ranking, so it appears that dominance is not greatly affected by injury status. Zana may be the only example, as she is an older female, and so should be ranked higher, since age has been discussed as the most likely determinate of female dominance (Nishida 1989).

**Table A2.1** Observed dominance interactions between adult females in present study and Fawcett's (2000) study and estimation of age of female.

<i>Name of Subject</i>	<i>Number of subjects observed being dominant over</i>	<i>Name of those subjects</i>	<i>Estimation of rank</i>	<i>Estimation of age</i>
Nambi	8	Kigere, Kutu, Kalema, Banura, Zana, Kewayaya, Janie, Kwera	High	Older
Zimba	4	Kwera, Kalema, Zana, Janie	High	Older
Kigere	3	Kutu, Ruda, Janie	High	Older
Kutu	1	Kalema	Middle/High	Younger
Janie	2	Kutu, Kwera	Middle/High	Younger
Kwera	4	Zana, Kewayaya, Kalema, Janie	Middle	Younger
Ruda	1	Zana	Middle	Older
Ruhara	2	Kalema, Banura	Middle	Older
Banura	1	Janie	Middle	Older
Zana	1	Janie	Middle/Low	Older
Kewayaya	0		Low	Younger
Kalema	0		Low	Younger

Estimation of age is based on data from the senior field assistant at Budongo Forest Project, 1996.



## References

- Albrecht, H. 1976. Chimpanzees in Uganda. *Oryx* **13**:357-361.
- Altmann, J. 1974. Observational Study of Behaviour: Sampling Methods. *Behaviour* **49**:227-267.
- Ammann, K. 2001. Bushmeat Hunting and the Great Apes. Pages 71-85 in B. Beck, T. Stoinski, M. Hutchins, T. Maple, B. Norton, A. Rowan, E. Stevens, and A. Arluke, editors. *Great Apes and Humans*. Smithsonian Institution Press, Washington and London.
- Archabald, K., and L. Naughton-Treves. 2001. Tourism revenue-sharing around National Parks in western Uganda: early efforts to identify and reward local communities. *Environmental Conservation* **28**:135-149.
- Arnold, K. 2001. Affiliation, aggression and reconciliation in male chimpanzees. School of Psychology. University of St. Andrews. PhD thesis.
- Assersohm, C. 1999. Development of Foraging in Wild Chimpanzees. University of St. Andrews. PhD thesis.
- Assersohm, C., and A. Whiten. 1999. Food sharing between mother and infant chimpanzees in the wild: beggars can be choosers. *Folia Primatologica* **70**:226.
- Babweteera, F., A. Plumptre, and J. Obua. 2000. Effect of gap size and age on climber abundance and diversity in Budongo Forest Reserve, Uganda. *African Journal of Ecology* **38**:230-237.
- Baker, K., and B. B. Smuts. 1994. Social Relationships of Female Chimpanzees. pages 227-242 in R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne, editors. *Chimpanzee Cultures*. Harvard University Press, Cambridge, Massachusetts.
- Boesch, C. 1991a. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* **117**:220-242.
- Boesch, C. 1991b. Handedness in wild chimpanzees. *International Journal of Primatology* **12**:541-558.
- Boesch, C. 1996. Social grouping in Tai chimpanzees. Pages 101-113 in W. C. McGrew, L. F. Marchant, and T. Nishida, editors. *Great Ape Societies*. Cambridge University Press, Cambridge.
- Boesch, C. 1997. Evidence for dominant wild female chimpanzees investing more in sons. *Animal Behaviour* **54**:811-815.
- Boesch, C., and H. Boesch-Achermann 2000. *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford University Press, Oxford.



- Boinski, S., A. Treves, and C. A. Chapman. 2000. A critical evaluation of the influence of predators: effects on group travel. Pages 43-72 in S. Boinski, and P. A. Garber, editors. *On the Move: How and Why Animals Travel in Groups*. The University of Chicago Press, Chicago and London.
- Brent, L., C. A. Bramblett, K. A. Bard, M. A. Bloomsith, and J. Blangero. 1997. The influence of siblings on wild infant chimpanzee social interaction. *Behaviour* **134**:1189-1210.
- Brownlow, A. R., A. Plumptre, V. Reynolds, and R. Ward. 2001. Sources of variation in the nesting behaviour of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *American Journal of Primatology* **55**:49-55.
- Bryne, R. W., and J. M. E. Byrne. 1991. Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla g. beringei*). *Cortex* **27**:521-546.
- Bshary, R. 2001. Diana monkeys, *Cercopithecus diana*, adjust their anti-predator response behaviour to human hunting strategies. *Behavioral Ecology and Sociobiology* **50**:251-256.
- Bygott, D. 1979. Agonistic behaviour, dominance and social structure in wild chimpanzees of the Gombe National Park. Pages 405-428 in D. A. Hamburg, and E. R. McCown, editors. *The Great Apes*. Benjamin/Cummings, Menlo Park.
- Chapman, C. A., A. Gautier-Hion, J. Oates, and D. A. Onderdonk. 1999. African primate communities: determinants of structure and threats to survival. Pages 1-37 in J. G. Fleagle, C. H. Janson, and K. E. Reed, editors. *Primate Communities*. Cambridge University Press, Cambridge.
- Dale, S., K. Mork, R. Solvang, and A. Plumptre. 2000. Edge effects on the understorey bird community in a logged forest in Uganda. *Conservation Biology* **14**:265-276.
- Davidian, M., and D. M. Giltinan 1995. *Nonlinear Models for Repeated Measurement data*. Chapman & Hall, London.
- de Waal, F. B. M. 1982. *Chimpanzee Politics - Power and Sex among the Apes*. Jonathon Cape, London.
- de Waal, F. B. M. 1996. *Good natured - the origins of right and wrong in humans and other animals*. Harvard University Press, Cambridge, Massachusetts.
- Dettwyler, K. A. 1991. Can paleopathology provide evidence for "compassion"? *American Journal of Physical Anthropology* **84**:375-384.
- DiBitetti, M. S. 1997. Evidence for an important social role of allogrooming in a platyrrhine primate. *Animal Behaviour* **54**:199-211.

- Doran, D. M. 1993. Sex differences in adult chimpanzee positional behaviour: the influence of body size on locomotion and posture. *American Journal of Physical Anthropology* **91**:99-115.
- Doran, D. M. 1997. Influence of seasonality on activity patterns, feeding behaviour, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology* **18**:183-206.
- Doran, D. M., and K. D. Hunt. 1994. Comparative locomotor behaviour of chimpanzees and bonobos - species and habitat differences. Pages 93-108 in R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne, editors. *Chimpanzee Cultures*. Harvard University Press, Cambridge, Massachusetts.
- Dranzoa, C., E. Sande, I. Owionji, and A. Plumptre. 1997. A survey of Nahan's francolin *Francolinus nahani* in two tropical rainforests of Uganda. *African Bird Club* **4**:90-92.
- Dunbar, R. I. M. 1988. *Primate Social Systems: studies in behavioral adaptation*. Croom Helm, London and Sydney.
- Edroma, E. L., N. Rosen, and P. S. Miller. 1997. Conserving the Chimpanzees of Uganda: Population and Habitat Viability Assessment for *Pan troglodytes schweinfurthii*. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota.
- Eggeling, W. J. 1947. Observations on the ecology of the Budongo Rain Forest, Uganda. *Journal Of Ecology* **34**:24-87.
- Fairgrieve, C. 1995. Infanticide and infant eating in the blue monkey (*Cercopithecus mitis stuhlmanni*) in the Budongo Forest Reserve, Uganda. *Folia Primatologica* **64**:69-72.
- FAO. 1999. State of the World's Forests. Food and Agriculture Organisation of the United Nations, Rome.
- Fawcett, K. 2000. Female relationships and food availability in a forest community of chimpanzees. University of Edinburgh. PhD thesis.
- Fawcett, K., and G. Muhumuza. 2000. Death of a wild chimpanzee community member: possible outcome of intense sexual competition. *American Journal of Primatology* **51**:243-247.
- Fossey, D. 1981. A grim struggle for survival: the imperiled Mountain Gorilla. *National Geographic* **159**:500-523.
- Fossey, D. 1985. *Gorillas in the Mist*. Penguin Books Ltd, England.

- Frayer, D. W., W. A. Horton, R. Macchiarelli, and M. Mussi. 1987. Dwarfism in an adolescent from the Italian later Upper Palaeolithic. *Nature* **330**:60-62.
- Ghiglieri, M. P. 1984. *The Chimpanzees of Kibale Forest: A Field Study of Ecology and Social Structure*. Columbia University Press, New York.
- Ghiglieri, M. P. 1988. *East of the Mountains of the Moon - Chimpanzee Society in the African Rainforest*. The Free Press, New York.
- Gonder, M. K., J. F. Oates, T. R. Disotell, M. R. Forstner, J. C. Morales, and D. J. Melnick. 1997. A new west African chimpanzee subspecies? *Nature* **338**:337.
- Goodall, J. 1967. Mother-offspring relationships in free-ranging chimpanzees. Pages 287-346 in D. Morris, editor. *Primate Ethology*. Weidenfeld and Nicolson, London.
- Goodall, J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs* **1**:161-311.
- Goodall, J. 1986. *The Chimpanzees of Gombe - Patterns of Behaviour*. Harvard University Press, Cambridge, Massachusetts.
- Gordon, A. D. 1999. *Classification*. Second Edition. Chapman and Hall/CRC, London.
- Groves, C. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington and London.
- Halperin, S. D. 1979. Temporary association patterns in free ranging chimpanzees. Pages 490-499 in D. A. Hamburg, and E. R. McCown, editors. *The Great Apes*. The Benjamin/Cummings Publishing Company, California.
- Hashimoto, C. 1999. Snare Injuries of Chimpanzees in the Kalinzu Forest, Uganda. *Pan Africa News* **6**:20-22.
- Hashimoto, C., T. Furuichi, and Y. Tashiro. 2001. What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. *International Journal of Primatology* **22**:947-959.
- Hayaki, H. 1985. Social play of juvenile and adolescent chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates* **26**:343-360.
- Hayaki, H. 1988. Association partners of young chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates* **29**:147-161.
- Hemelrijk, C., and C. H. de Kogel. 1989. What chimpanzee mothers have more sociable infants? *Behaviour* **111**:305-318.



- Hill, C. M. 2000. Conflict interest between people and baboons: crop raiding in Uganda. *International Journal of Primatology* **43**:77-84.
- Hiraiwa-Hasegawa, M. 1990a. Maternal investment before weaning. Pages 257-266 in T. Nishida, editor. *The Chimpanzees of the Mahale Mountains - Sexual and Life History Strategies*. University of Tokyo Press, Tokyo.
- Hiraiwa-Hasegawa, M. 1990b. Role of food sharing between mother and infant in the ontogeny of feeding behaviour. Pages 267-275 in T. Nishida, editor. *The Chimpanzees of the Mahale Mountains - Sexual and Life History Strategies*. University of Tokyo Press, Tokyo.
- Hiraiwa-Hasegawa, M., R. W. Byrne, H. Takasaki, and J. M. E. Byrne. 1986. Aggression towards large carnivores by wild chimpanzees of Mahale Mountains National Park, Tanzania. *Folia Primatologica* **47**:8-13.
- Horvat, J. R., and H. C. Kraemer. 1981. Infant socialisation and maternal influence in chimpanzees. *Folia Primatologica* **36**:99-110.
- Howard, P. 1991. Nature Conservation in Uganda's Tropical Forest Reserves. IUCN, Gland, Switzerland
- Howard, P. C., F. W. Davenport, P. V. Kigenyi, M. C. Baltzer, C. J. Dickinson, J. Lwanga, R. A. Matthews, and E. Mupada. 2000. Protected area planning in the tropics: Uganda's national system of forest nature reserves. *Conservation Biology* **14**:858-875.
- Howell, D. C. 1997. *Statistical Methods for Psychology*. Duxbury Press, New York.
- Huffman, M., and R. W. Wrangham. 1994. Diversity of medicinal plant use by chimpanzees in the wild. Pages 129-148 in R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne, editors. *Chimpanzee Cultures*. Harvard University Press, Cambridge and London.
- Hunt, K. D., and W. C. McGrew. 2002. Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. Pages 35-51 in C. Boesch, G. Hohmann, and L. F. Marchant, editors. *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge University Press, Cambridge.
- Hutchins, M., and D. P. Barash. 1976. Grooming in primates: implications for its utilitarian function. *Primates* **17**:145-150.
- Isabirye-Basuta, G. 1988. Food competition among individuals in a free-ranging chimpanzee community in Kibale Forest, Uganda. *Behaviour* **105**:135-147.
- Isabirye-Basuta, G. 1989. Feeding ecology of chimpanzees in the Kibale Forest, Uganda. Pages 116-127 in P. G. Heltne, and L. A. Marquardt, editors.

*Understanding Chimpanzees*. Harvard University Press, Cambridge, Massachusetts.

Itani, J., and A. Suzuki. 1967. The social unit of chimpanzees. *Primates* 8:355-381.

Jaccard, J., and M. A. Becker 1990. *Statistics for the Behavioral Sciences*. Wadsworth Publishing Company, Belmont, California.

Johnson, K. 1996. Hunting in the Budongo Forest, Uganda. *SWARA* 19:24-26.

Kano, T. 1984. Observations of physical abnormalities among the wild bonobos (*Pan paniscus*) of Wamba, Zaire. *American Journal of Physical Anthropology* 63:1-11.

Kanyuyni Basabose, A. 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology* 58:1-21.

Kawanaka, K. 1989. Age differences in social interactions of young males in a chimpanzee unit-group at the Mahale Mountains National Park, Tanzania. *Primates* 30:285-305.

Kawanaka, K. 1993. Age differences in the spatial positioning of males in a chimpanzee unit-group at the Mahale Mountains National Park, Tanzania. *Primates* 34:255-270.

Kortlandt, A. 1962. Chimpanzees in the Wild. *Scientific American* 206:128-138.

Lloyd, J., and S. Mugume. 2000. Investigation into the survival of a small chimpanzee community under immediate threat. Jane Goodall Institute, Uganda. Unpublished Report.

Marriott, H. 1996. Micro-demography of a farming population of western Uganda: a preliminary analysis investigating population pressure on the Budongo Forest Reserve. Budongo Forest Project report # 32. Unpublished report.

Matsumoto-Oda, A. 1999. Mahale chimpanzees: grouping patterns and cycling females. *American Journal of Primatology* 47:197-207.

Matsumoto-Oda, A., K. Hosaka, M. Huffman, and K. Kawanaka. 1998. Factors affecting party size in chimpanzees of the Mahale Mountains. *International Journal of Primatology* 19:999-1011.

Matsumoto-Oda, A., and R. Oda. 1998. Changes in the activity budget of cycling female chimpanzees. *American Journal of Primatology* 46:157-166.

McCullagh, P., and J. A. Nelder 1989. *Generalized Linear Models*. Chapman & Hall, London.

- Mitani, J. C., and D. P. Watts. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour* **61**:915-924.
- Moeller, W. 2000. Chimp meat in western Uganda. Ugandan Wildlife Education Centre. Unpublished Report.
- Mudakikwa, A. B., M. R. Cranfield, J. M. Sleeman, and U. Eilenberger. 2001. Clinical medicine, preventive health care and research on mountain gorillas in the Virunga Volcanoes region. Chapter 13 in M. M. Robbins, P. Sicotte, and K. J. Stewart, editors. *Mountain Gorillas: three decades of research at Karisoke*. Cambridge University Press, Cambridge.
- Muller, M. N. 2000. The Knuckle-Walking Wounded. *Natural History* **109**:44-46.
- Munn, J., and G. Kalema. 1999-2000. Death of a chimpanzee *Pan troglodytes schweinfurthii* in a trap in Kasokwa Forest Reserve, Uganda. *African Primates* **4**:58-61.
- Muroyama, Y., and Y. Sugiyama. 1994. Grooming relationships in two species of chimpanzees. Pages 169-180 in R. W. Wrangham, W. C. McGrew, F. B. M. d. Waal, and P. G. Heltne, editors. *Chimpanzee Cultures*. Harvard University Press, Cambridge, Massachusetts.
- Nakagawa, N., T. Iwamoto, N. Yokota, and A. G. Soumah. 1996. Inter-regional and inter-seasonal variations of food quality in Japanese macaques: constraints of digestive volume and feeding time. Pages 207-234 in J. E. Fa, and D. G. Lindburg, editors. *Evolution and ecology of macaque societies*. Cambridge University Press, Cambridge.
- Nakamichi, M., H. Fujii, and T. Koyama. 1983a. Behavioural development of a malformed infant in a free-ranging group of Japanese monkeys. *Primates* **24**:52-66.
- Nakamichi, M., H. Fujii, and T. Koyama. 1983b. Development of a congenitally malformed Japanese monkey in a free ranging group during the first four years of life. *American Journal of Primatology* **5**:205-210.
- Nakamichi, M., H. Nobuhara, T. Nobuhara, M. Nakahashi, and H. Nigi. 1997. Birth rates and mortality rates of infants with congenital malformations of the limbs in the Awajishima free-ranging group of Japanese monkeys (*Macaca fuscata*). *American Journal of Primatology* **42**:225-234.
- Napier, J. R., and P. H. Napier 1985. *The Natural History of the Primates*. Cambridge University Press., Cambridge.
- NEMA 1999. *State of the Environment Report for Uganda 1998*. National Environment Management Authority (NEMA), South Africa.



- Newton-Fisher, N. 1997. Tactical behaviour and decision making in wild chimpanzees. Cambridge University. PhD thesis.
- Newton-Fisher, N. 1999a. Association by male chimpanzees: a social tactic? *Behaviour* **136**:705-730.
- Newton-Fisher, N. 1999b. The diet of chimpanzees in the Budongo Forest Reserve. *African Journal of Ecology* **37**:344-354.
- Newton-Fisher, N. 1999c. Infant killers of Budongo. *Folia Primatologica* **70**:167-169.
- Newton-Fisher, N. 1999d. Termite eating and food sharing by male chimpanzees in the Budongo Forest, Uganda. *African Journal of Ecology* **37**:369-371.
- Newton-Fisher, N., V. Reynolds, and A. Plumptre. 2000. Food supply and Chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest Reserve, Uganda. *International Journal of Primatology* **21**:613-628.
- Nicholson, N. A. 1987. Infants, mothers and other females. Pages 330-342 in D. L. C. B.B. Smuts, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker., editor. *Primate Societies*. University of Chicago Press, Chicago.
- Nishida, T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* **9**:167-224.
- Nishida, T. 1979. The social structure of chimpanzees of the Mahale Mountains. Pages 73-122 in D. A. Hamburg, and E. R. McCown, editors. *The Great Apes*. Benjamin/Cummings, Menlo Park, Calif.
- Nishida, T. 1983. Alloparental behaviour in wild chimpanzees of the Mahale Mountains, Tanzania. *Folia Primatologica* **41**:1-33.
- Nishida, T. 1988. Development of social grooming between mother and offspring in wild chimpanzees. *Folia Primatologica* **50**:109-123.
- Nishida, T. 1989. Social interactions between resident and immigrant female chimpanzees. Pages 68-89 in P. G. Heltne, and L. A. Marquardt, editors. *Understanding Chimpanzees*. Harvard University Press, Cambridge, Massachusetts.
- Nishida, T. 1990. A quarter century of research in the Mahale Mountains: an overview. Pages 3-36 in T. Nishida, editor. *The Chimpanzees of the Mahale Mountains - Sexual and Life History Strategies*. University of Tokyo Press, Tokyo.
- Nishida, T., H. Takasaki, and Y. Takahata. 1990. Demography and reproductive profiles. Pages 63-98 in T. Nishida, editor. *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*. University of Tokyo Press, Tokyo.

- Notman, H., and J. Munn. 2003. A case of infant carrying by an adult male chimpanzee in the Budongo Forest (in press). *Pan Africa News* **10** (1).
- Oates, J. F. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology* **21**:1-9.
- Obua, J., A. Y. Banana, and N. Turyahabwe. 1998. Attitudes of local communities towards forest management practices in Uganda: the case of Budongo Forest Reserve. *Commonwealth Forestry Review* **77**:113-118.
- Owiunji, I., and A. Plumptre. 1998. Bird communities in logged and unlogged compartments in Budongo Forest, Uganda. *Forest Ecology and Management* **108**:115-126.
- Paterson, J. D. 1992. *Primate Behaviour - an exercise workbook*. Waveland Press, Illinois.
- Paterson, J. D. 1997. Seed predation patterns in the diet of the Sonso forest baboon troop. *American Journal of Primatology* **42**:140.
- Pepper, J. W., J. C. Mitani, and D. P. Watts. 1999. General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology* **20**:613-632.
- Plumptre, A. 1996. Changes following 60 years of selective timber harvesting in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management* **89**:101-113.
- Plumptre, A., S. Mugume, D. Cox, and C. Montgomery. 2001. Chimpanzee and large mammal survey of Budongo Forest Reserve and the Kibale National Park. Jane Goodall Institute and Wildlife Conservation Society, New York.
- Plumptre, A., S. Mugume, C. D., R. Bergl, and L. Rothen. 1999. Chimpanzee and other large mammals survey of Bugoma Forest Reserve and the Kagombe-Matiri Forest reserve complex. Jane Goodall Institute and Wildlife Conservation Society, New York.
- Plumptre, A., and V. Reynolds. 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *Journal of Applied Ecology* **31**:631-641.
- Plumptre, A., and V. Reynolds. 1996. Censusing chimpanzees in the Budongo Forest, Uganda. *International Journal of Primatology* **17**:85-99.
- Plumptre, A., and V. Reynolds. 1997. Nesting behaviour of chimpanzees: implications for censuses. *International Journal of Primatology* **18**:475-485.



- Plumptre, A. J., D. Cox, and S. Mugume. 2003. The Status of Chimpanzees in Uganda. Wildlife Conservation Society, Albertine Rift Technical Reports Number 2.
- Poppenwimer, C. J. 1999-2000. Encounter in Uganda between chimpanzees *Pan troglodytes* and a leopard *Panthera pardus*. *African Primates* 4:75-76.
- Pusey, A. 1976. Age changes in the mother-offspring association of wild chimpanzees. Pages 119-123 in D. J. Chivers, and J. Herbert, editors. *Recent Advances in Primatology*. Academic Press, London.
- Pusey, A. 1983. Mother-offspring relationships in chimpanzees after weaning. *Animal Behaviour* 31:363-377.
- Pusey, A., J. Williams, and J. Goodall. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277:828-831.
- Putman, J. J. 1988. The search for modern humans. *National Geographic* 174:438-477.
- Quiatt, D. 1996. Budongo Forest Chimpanzees: Behavioural accommodations to physical disabilities (Ms. only). Paper presented at the XVIth Congress of the International Primatological Society, Madison, Wisconsin.
- Quiatt, D., and Z. Kiwede. 1994. An observation of leaf sponge drinking by a Budongo Forest Chimpanzee. *American Journal of Primatology* 33:236.
- Quiatt, D., and V. Reynolds. 1994. Budongo Forest chimpanzees: composition of feeding groups during the rainy season, with attention to the social integration of disabled individuals. Abstract XVth Congress of the International Primatological Society, Bali, Indonesia.
- Quiatt, D., B. Rutan, T. Stone, and V. Reynolds. 1994. Budongo Forest chimpanzees: composition of feeding groups during the rainy season, with attention to the spatial integration of disabled individuals. Pages 1-13. Budongo Forest Project. Unpublished Report.
- Reynolds, V. 1963. An outline of the behaviour and social organisation of forest living chimpanzees. *Folia Primatologica*. 1:95-102.
- Reynolds, V. 1965. *Budongo - A Forest and its Chimpanzees*. Methuen & Co, London.
- Reynolds, V. 1990. Conservation of chimpanzees in the Budongo Forest Reserve. *Primate Conservation* 11:41-43.
- Reynolds, V. 1993. Sustainable forestry: the case of the Budongo Forest, Uganda. *SWARA* 16:13-17.



- Reynolds, V. 1997/8. Demography of Chimpanzees *Pan troglodytes schweinfurthii* in Budongo Forest, Uganda. *African Primates* 3:25-28.
- Reynolds, V., and F. Reynolds. 1965. Chimpanzees of the Budongo Forest. Pages 368-424 in I. De Vore, editor. *Primate Behaviour - Field Studies of Monkeys and Apes*. Holt, Rinehart and Winston, New York.
- Rijt-Plooij, H. H. C. v. d., and F. X. Plooij. 1988. Mother-infant relations, conflict, stress and illness among free-ranging chimpanzees. *Developmental Medicine and Child Neurology* 30:306-315.
- Schaller, G. 1963. *The Mountain Gorilla*. University of Chicago Press, Chicago.
- Seyfarth, R. M. 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour* 28:798-813.
- Sherrow, H. M. 2001. Adolescent male chimpanzee grooming behaviour at Ngogo, Kibale National Park, Uganda. *American Journal of Physical Anthropology* 114:136.
- Silk, J. B., and H. C. Kraemer. 1976. Comparison of mother-infant proximity among wild and captive chimpanzees. Pages 115-117 in D. J. Chivers, and J. Herbert, editors. *Recent Advances in Primatology*. Academic Press, London.
- Simpson, M. 1973. The social grooming of male chimpanzees. Pages 411-505 in R. Michael, and J. Crook, editors. *Comparative Ecology and Behaviour in Primates*. Academic Press, New York.
- Smith, R. 1995. Some effects of limb injuries on the chimpanzees of the Budongo Forest. Pages 1-8. Budongo Forest Project Report. Unpublished Report.
- Solecki, R. S. 1971. *Shanidar: the first flower people*. Alfred A. Knopf, New York.
- Spini, L. 1998. The frequency and significance of social grooming in the Sonso community of chimpanzees at the Budongo Forest, Uganda. University of Oxford. Masters thesis.
- Stanford, C., J. Wallis, E. Mpongo, and J. Goodall. 1994. Hunting decisions in wild chimpanzees. *Behaviour* 131:1-18.
- Sterck, E. H. M., D. P. Watts, and C. P. van Schaik. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology* 41:291-309.
- Stokes, E. J. 1999. Feeding skills and the effect of injury on wild chimpanzees. University of St. Andrews. PhD thesis.

- Stokes, E. J., and R. W. Byrne. 2001. Cognitive capacities for behavioural flexibility in wild chimpanzees (*Pan troglodytes*): the effect of snare injury on complex manual food processing. *Animal Cognition* 4:11-28.
- Sugiyama, Y. 1968. Social organisation of chimpanzees in the Budongo Forest, Uganda. *Primates* 9:225-258.
- Sugiyama, Y. 1969. Social behaviour of chimpanzees in the Budongo Forest, Uganda. *Primates* 10:197-225.
- Sugiyama, Y. 1979. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* 20:323-339.
- Sugiyama, Y. 1981. Observations on the population dynamics and behaviour of wild chimpanzees at Bossou, Guinea, in 1979-1980. *Primates* 22:435-444.
- Sugiyama, Y. 1988. Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. *International Journal of Primatology* 9:393-407.
- Suzuki, A. 1971. On the problems of conservation of the chimpanzees in east Africa and of the preservtaion of their environment. *Primates* 12:415-418.
- Suzuki, A. 1979. The variation and adaptation of social groups of chimpanzees and black and white colobus monkeys. Pages 153-173 in S. Bernstein, and E. Smith, editors. *Primate Ecology and Human Origins*.
- Takahata, Y. 1990. Social relationships among adult males. Pages 149-170 in T. Nishida, editor. *The Chimpanzees of the Mahale Mountains - Sexual and Life History Strategies*. University of Tokyo Press, Japan.
- Teleki, G. 1989. Population status of wild chimpanzees (*Pan troglodytes*) and threats to survival. Pages 311-353 in P. G. Heltne, and L. A. Marquardt, editors. *Understanding Chimpanzees*. Harvard University Press, Cambridge.
- Thompson, W. A. R. 1984. *Blacks Medical Dictionary*. Adams and Charles Black, London.
- Treves, A. 1999. Has predation shaped the social systems of arboreal primates? *International Journal of Primatology* 20:35-67.
- Tsukahara, T. 1993. Lions eat chimpanzees: the first evidence of predation by lions on wild chimpanzees. *American Journal of Primatology* 29:1 - 11.
- Tutin, C. E. G. 1980. Reproductive behaviour of wild chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility, Supplement* 28:43-57.

- Tutin, C. E. G., and M. Fernandez. 1991. Responses of wild chimpanzees and gorillas to the arrival of primatologists: behaviour observed during habituation. Pages 187-197 in H. O. Box, editor. *Primate Responses to Environmental Change*. Chapman and Hall, London.
- Wagner, T. 2000. Influence of forest type and tree species on canopy-dwelling beetles in Budongo Forest, Uganda. *Biotropica* **32**:502-514.
- Waller, J. C. W. 1995. The aetiologies of major limb injuries amongst chimpanzees in the Sonso area of the Budongo Forest, Uganda. University of Oxford. Masters thesis.
- Waller, J. C. W., and V. Reynolds. 2001. Limb injuries resulting from snares and traps in chimpanzees (*Pan troglodytes schweinfurthii*) of the Budongo Forest, Uganda. *Primates* **42**:135-139.
- Wallis, J. 1992. Chimpanzee genital swelling and its role in the pattern of sociosexual behavior. *American Journal of Primatology* **28**:101-113.
- Wallis, J. 1997. A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility* **109**:297-307.
- Wallis, J., and J. Goodall. 1993. Anogenital swelling in pregnant chimpanzees of Gombe National Park. *American Journal of Primatology* **31**:89-98.
- Wallis, J., and D. R. Lee. 1999. Primate conservation: prevention of disease transmission. *International Journal of Primatology* **20**:803-826.
- Watts, D. P. 2000a. Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology* **21**:189-210.
- Watts, D. P. 2000b. Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. *International Journal of Primatology* **21**:211-237.
- Watts, D. P., and A. E. Pusey. 1993. Behaviour of juvenile and adolescent great apes. Pages 148-167 in M. E. Pereira, and L. A. Fairbanks, editors. *Juvenile Primates - Life History, Development and Behaviour*. Oxford University Press, New York.
- White, F. J., and M. A. Burgman. 1990. Social organisation of the pygmy chimpanzee (*Pan paniscus*): multivariate analysis of intracommunity associations. *American Journal of Physical Anthropology* **83**:193-201.
- White, F. J., and R. W. Wrangham. 1988. The feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour* **105**:148-164.



- Whiten, A., J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C. E. G. Tutin, R. W. Wrangham, and C. Boesch. 1999. Cultures in Chimpanzees. *Nature* 399:682-685.
- Wilkie, D. S., J. G. Sidle, and G. C. Boundzanga. 1992. Mechanised logging, market hunting, and a bank loan in Congo. *Conservation Biology* 6:570-580.
- Williamson, L. 2000. Peace, poaching and streetwise gorillas. Pages 1-3. Dian Fossey Gorilla Fund International. Unpublished Report.
- Wrangham, R. W. 2001. Moral decisions about wild chimpanzees. Pages 230-244 in B. Beck, T. Stoinski, M. Hutchins, T. Maple, B. Norton, A. Rowan, E. Stevens, and A. Arluke, editors. *Great Apes and Humans the Ethics of Coexistence*. Smithsonian Institution Press, Washington.
- Wrangham, R. W., C. A. Chapman, A. P. Clark-Arcadi, and G. Isabirye-Basuta. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. Pages 45-57 in W. C. McGrew, L. F. Marchant, and T. Nishida., editors. *Great Ape Societies*. Cambridge University Press, Cambridge.
- Wrangham, R. W., A. P. Clark, and G. Isabirye-Basuta. 1992. Female social relationships and social organisation of Kibale Forest Chimpanzees. *Topics in Primatology*. University of Tokyo, Tokyo.
- Wrangham, R. W., and S. Mugume. 2000. Snare removal program in Kibale National Park: a preliminary report. *Pan Africa News* 7:18-20.
- Wrangham, R. W., and B. B. Smuts. 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproductive Fertility, Supplement* 28:13-31.